Effects of load and emotional state on EEG alpha-band power and inter-site synchrony during a visual working memory task

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Abstract

Motivationally/emotionally engaging stimuli are strong competitors for the limited capacity of sensory and cognitive systems. Thus, they often act as distractors, interfering with performance in concurrent primary tasks. Keeping task-relevant information in focus while suppressing the impact of distracting stimuli is one of the functions of working memory (WM). Macroscopic brain oscillations in the alpha band (8–13 Hz) have recently been identified as a neural correlate of WM processing. Using electroencephalography, we examined the extent to which changes in alpha power and inter-site connectivity during a typical WM task are sensitive to load and emotional distraction. Participants performed a lateralized change-detection task with two levels of load (four vs. two items), which was preceded by naturalistic scenes rated either as unpleasant or neutral, acting as distractors. The results showed the expected parieto-occipital alpha reduction in the hemisphere contralateral to the WM task array, compared to the ipsilateral hemisphere, during the retention interval. Selectively heightened oscillatory coupling between frontal and occipital sensors was observed (1) during the retention interval as a function of load, and (2) upon the onset of the memory array, after viewing neutral compared to unpleasant distractors. At the end of the retention interval, we observed greater coupling during the unpleasant compared to the neutral condition. These findings are consistent with the notions that (1) representing more items in WM requires greater interconnectivity across cortical areas, and (2) unpleasant emotional distractors interfere with subsequent WM processing by disrupting processing during the encoding stage.

Keywords Working memory · EEG · Alpha oscillations · Inter-site synchrony · Emotion

Introduction

Working memory (WM) can be described as a set of cognitive processes that allow us to maintain a limited amount of goal-relevant information, even when this information is no longer present in the sensory environment (Baddeley, 2012; Cowan, 2001). In order to successfully access and manipulate WM content, these processes rely not only on maintaining and selecting information, but also on suppressing irrelevant and

distracting items (Luria, Balaban, Awh, et al., 2016). A substantial body of studies have used lateralized change-detection tasks to characterize the neural mechanisms underlying WM processing (e.g., Stout, Shackman, & Larson, 2013; Vogel, McCollough, & Machizawa, 2005; Vogel, & Machizawa, 2004). In a typical version of this task, two sequential bilateral arrays are shown and participants are asked to remember the first array (the memory set) in the pre-cued hemifield (see, e.g., Qi, Chen, Hitchman, et al., 2014), then after a retention interval, participants are asked to compare the array held in WM (the memory set) with the second array (the test set) while maintaining fixation.

Previously, we used a lateralized WM change-detection task to investigate the extent to which a sustained unpleasant emotional state affects WM capacity, as indexed by the event-related potential (ERP) referred to as Contralateral Delay Activity (CDA; Figueira, Oliveira, Pereira, et al., 2017). To examine the effect of emotional/motivational states on WM processing, participants viewed neutral or unpleasant pictures before each trial within a blocked design. Participants showed

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the typical CDA enhancement when remembering four items, compared to two items, only during blocks in which all-neutral pictures were presented. By contrast, the CDA amplitude did not vary with set size during the unpleasant emotional state, which was induced by viewing all-unpleasant pictures. These results dovetail with previous studies that suggest that the processing of task-relevant stimuli is impaired when emotional distractors are presented before high-demanding cognitive tasks (Ihssen, Heim, & Keil, 2007; Pereira, Volchan, de Souza, et al., 2006).

Despite the fact that ERP studies have been critical in highlighting the temporal structure of WM processing (see, e.g., Perez & Vogel, 2012), the ERP technique has limitations, for example, in defining inter-site interactions as well as in characterizing neural processes that are not time-locked to the event of interest. Particularly these latter processes may provide links to neural recordings obtained in the animal model, such as recordings of local field potentials during WM tasks in monkeys (Bastos, Loonis, Kornblith, et al., 2018; Lee, Simpson, Logothetis, et al., 2005). One way to address these limitations is to consider large-scale oscillatory activity contained in the human electroencephalogram (EEG) signal. A substantial body of research has identified specific time-frequency properties of oscillatory phenomena in the human EEG, which are sensitive to experimental manipulations in cognitive tasks, including WM tasks (Freunberger, Werkle-Bergner, Griesmayr, et al., 2011; Roux & Uhlhaas, 2014).

The present study examines neural mass oscillatory activity recorded from the scalp using EEG, with a focus on oscillations in the alpha frequency band (8–12 Hz). Changes in alpha power, phase, and inter-site phase locking have been related to a range of neurophysiological and cognitive processes. For example, heightened alpha power has been linked to the selective inhibition of local cortical processing (Palva & Palva, 2011), potentially in the service of distractor suppression, ultimately contributing to attentive selection (Foxe & Snyder, 2011). Other work has prompted the hypothesis that alpha oscillations temporally scaffold cortical processing in a pulsed fashion where one phase of the alpha cycle is associated with inhibition and another with the excitation of neuronal activity (Mathewson et al., 2009). Overall, it is now widely accepted that the active sensory processing of external stimuli prompts alpha power reduction, whereas tasks that require suppression of sensory input or focusing on internal representations prompt alpha power enhancement. Thus, time-varying alpha power and alpha-band connectivity (see below) are promising indices for characterizing WM dynamics, especially in the context of distraction and interference exerted by salient emotional stimuli.

Previous EEG studies have observed modulations in the alpha band during WM tasks (Jensen, Gelfand, Kounios, et al., 2002; Klimesch, Sauseng, & Hanslmayr, 2007). Based on a review of the literature, Klimesch et al. (2007) suggested

that oscillatory activity in the alpha range is selectively altered during different stages of WM processing. In line with this notion, many studies have shown, during the retention interval, decreased alpha-band power contralateral to an attended location and increased alpha-band power ipsilateral to an attended location during the retention interval (see, e.g., Sauseng, Klimesch, Heise, et al., 2009). This pattern of findings is in line with the notion that heightened alpha activity reflects suppression of processing task-irrelevant or distracting information (Foxe & Snyder, 2011). Thus, this asymmetry has been hypothesized to reflect differential excitability of cortical areas representing attended versus non-attended locations or features (Klimesch, 2012). Moreover, findings from trans-cranial magnetic stimulation (TMS) studies corroborate this hypothesis by demonstrating that TMS-evoked alpha oscillatory activity in task-relevant sensory areas is associated with decline in perceptual performance (Herring et al., 2015). Conversely, evoking alpha activity in regions ipsilateral to task-relevant items prompts improved distractor suppression (Sauseng et al., 2009).

Differential alpha power during anticipatory processing in lateralized WM tasks is thought to facilitate subsequent visual processing at the attended position while potentially reflecting “inhibitory” processes against the task-irrelevant positions’ visual input. Such an inhibitory function of relatively heightened alpha-band oscillations may represent a neural correlate of shifting attention away from task-irrelevant stimuli (Schneider, Barth, Haase, et al., 2019). Changes in the topography of alpha-band power may also be related to the encoding of specific spatial locations stored in WM (Foster, Sutterer, Serences, et al., 2016), which points to an overlap between spatial WM and spatial attention.

In addition to power changes in the alpha-band of the EEG, analyses of oscillatory activity provide an avenue to quantifying the temporal coupling between recordings from different locations. Oscillatory coupling has been defined as a mechanism for regulating and coordinating intra-areal processing and inter-areal interactions (Buzsáki, Logothetis, & Singer, 2013; Singer, 2009). Given their high amplitude, and their sensitivity to sensory, memory, and motor processes alpha-band oscillations in particular have been linked to long-range communication among cortical networks (Klimesch et al., 2007). For example, intracranial EEG recordings have shown frequency-specific coordination of distal cortical events at consistent time lags, and with stable center frequencies, at the alpha frequency (Chapeton, Haque, Wittig, Inati, & Zaghloul, 2019). Together, these data support the hypothesis that changes in alpha power and in inter-site phase connectivity across the scalp may systematically reflect changes in WM dynamics.

Inter-site phase-locking analyses quantify the consistency of the oscillatory phase across trials and recording sites, and have been used to test hypotheses regarding large-scale

interactions between cortical areas (Lachaux, Rodriguez, Martinerie, & Varela, 1999). Here, we use this metric to examine the extent to which visual WM processing is associated with fronto-occipital interactions in the alpha range, reflected in oscillatory phase coherence between frontal and occipital recording sites.

Although substantial evidence suggests that the frontal cortex is not a substrate of item storage in WM (e.g., Adam & Postle, 2013), there is empirical support for its role in actively focusing attention on the relevant sensory item's representation and in suppressing the sensory processing of potentially distracting items (Postle, 2006). For example, functional MRI (fMRI) evidence has converged to show that visual WM is supported by a network of frontal, temporal, parietal, and occipital cortices (Linden et al., 2003; Pessoa et al., 2002; Todd & Marois, 2004). Specifically, there is evidence to support that frontoparietal areas mediate attentional shifts towards relevant WM items whereas occipital areas are responsible for keeping these relevant stimuli in an active state (Konen & Kastner, 2008). Consistent with this notion, Sreenivasan, Curtis, and D'Esposito (2014) suggested that frontal activity may reflect top-down influences on sensory regions (such as visual cortex) during WM tasks. Additionally, increased phase synchronization in the alpha-band has been suggested to reflect the activity within cell assemblies involved in maintaining items in visual WM (Bonnefond & Jensen, 2012; Jensen et al., 2002). More recently, Lobier et al., (2018) measured long-range phase synchronization in the alpha range between the frontal and visual cortex. They demonstrated that this phase alignment may underlie visuospatial attention, which is known to be a key factor in WM processing (Gazzaley & Nobre, 2012).

Here we re-analyzed data from Figueira, Pacheco, Lobo, et al. (2018), who used a change-detection task with two levels of load (four vs. two items), preceded by an unpleasant or by a neutral stimulus. The present analysis focused on oscillatory EEG activity in the alpha range, which was examined both in terms of power and inter-site connectivity. Previous studies have characterized several robust alpha power effects during lateralized change-detection tasks, which we expected to replicate and extend. Notably, greater alpha reduction in the contralateral hemisphere compared to the ipsilateral hemisphere was observed previously (see, e.g., Sauseng et al., 2009). Additionally, Sauseng et al. (2009) demonstrated that parieto-occipital alpha activity varies with the set size in a similar bilateral change-detection task. Extending previous research, we aimed to: (1) characterize the effect of a leading emotional (vs. neutral) distractor on alpha power changes during lateralized WM processing, and to (2) define changes in fronto-occipital oscillatory coupling during the same task.

Emotional stimuli are processed in a prioritized fashion because of their relevance to survival (e.g., Öhman, Flykt, &

Esteves, 2001). Specifically, emotional stimuli show greater recruitment of visual brain areas when compared to neutral stimuli (Satpute et al., 2015). Such prioritization is believed to underlie interference effects due to the occupation of limited-capacity systems by emotionally engaging stimuli or due to an increased difficulty in disengaging attentional resources from emotional cues/information (Erthal, de Oliveira, Mocaiber, et al., 2005; Fernandes, Portugal, Alves, et al., 2013). Moreover, emotional states influence cognition (Oliveira, Mocaiber, David, et al., 2013) and storage of unpleasant distractor, and interfere with the representation of task-relevant information (Figueira et al., 2017; Stout et al., 2013). The interference effect caused by task-irrelevant emotional stimuli depends on the interaction between neural systems that allow the ability to stay focused on task-relevant information and systems involved in the processing of emotional information that may occupy WM (Iordan et al., 2013). The frontoparietal network is part of the neural models of WM and it is implicated in the maintenance of task-relevant information in mind. If WM is being occupied by emotionally irrelevant stimuli, frontoparietal resources important to execute top-down/cognitive control may be impaired (Botvinick & Braver, 2015).

Thus, we expected that the induction of an unpleasant emotional state (induced by viewing unpleasant, vs. neutral, pictures) interferes with the processing of the relevant items in the change-detection task, prompting perturbation in stimulus-evoked alpha asymmetry across set-size conditions. As an alternative hypothesis, the leading emotional distractor may differentially affect the set-size dependent contralateral alpha reduction, resulting in an interaction effect.

Additionally, to explore the role of top-down control feedback in mediating changes within the alpha-band activity throughout the experimental manipulations, we calculated the inter-site phase-locking index (ISPL) as a measure of functional connectivity between cortical areas (Lachaux et al., 1999). As our main goal, we determined the extent to which ISPL in the alpha-band between frontal and occipital electrode sensors would increase as a function of WM load (four vs. two items) and if this measure would be differently influenced by the participants' emotional state. Specifically, we expected greater fronto-occipital ISPL in the four-item condition, which would be consistent with the notion that top-down control between frontal and occipital visual areas is needed to cope with increasing difficulty. In terms of emotional effects, emotionally engaging stimuli can interfere not only with goal-directed behavior but specifically with WM capacity (Figueira et al., 2017; Stout et al., 2013). Thus, we expected that emotional engagement elicited by the unpleasant emotional state would disrupt the functional connectivity between frontal areas and the occipital visual areas.

Materials and methods

Participants

The final sample consisted of 28 participants (18 women; mean age: 21.89 years, $SD = 5.18$). Data sets of eight additional participants had to be excluded due to excessive extensive eye movements (three), excessive (more than 35%) behavioral errors (two), and excessive loss of electrophysiological data due to noise (more than 50% of bad trials) (three). The study sample size was modeled after a body of studies using similar measures and manipulations, with N s typically between 25 and 35, but no power analysis was conducted. Collection was stopped once this goal was reached. Future work will determine sample size based on simulations with extant data, across a range of effect sizes. The study procedure was approved by the local ethics committee and participants gave informed consent before the experimental session. All participants reported no history of neurological or psychiatric problems. They were all right-handed (according to Oldfield, 1971), and reported normal color vision and normal or corrected-to-normal visual acuity.

Stimuli and experimental procedure

To manipulate emotional engagement, we presented 120 pictures evenly distributed in two distinct emotional categories: unpleasant (mutilated bodies) and neutral (people in daily situations) presented in a blocked fashion. Pictures ($20^\circ \times 16^\circ$) were presented centrally on the screen before each trial. The pictures were taken from the International Affective Picture System (IAPS) (Lang, Bradley, & Cuthbert, 2008) and from the worldwide web. The neutral and unpleasant pictures differed significantly in both valence ($M = 5.06$, $SD = .42$ and $M = 2.08$, $SD = .52$, respectively, $t(59) = 35.06$; $P < 0.01$) and arousal ($M = 3.29$, $SD = 0.48$ and $M = 6.89$, $SD = 0.49$, respectively, $t(59) = -41.41$; $P < 0.01$).

The experiment consisted of four blocks, with 60 trials each. Two blocks comprised only neutral pictures, and two blocks comprised only unpleasant pictures. The block order was counter-balanced between participants with respect to emotional state. Participants were instructed that their task would begin after the picture disappeared in a given trial, but they were not instructed to ignore or to attend to the pictures. During the experimental session, participants were positioned 47 cm away from the screen on a head-and-chin rest.

Each trial began with a fixation cross that stayed on the screen throughout the block. After 2,000 to 2,100 ms from fixation cross onset (variable interval, rectangular distribution), a picture (neutral or unpleasant) was presented for 1,000 ms. After another variable interval (600–700 ms) after the picture offset, the WM change-detection task (Vogel et al., 2004) began (Fig. 1). Participants were instructed to respond

as quickly as possible, to avoid committing errors, and to maintain fixation. See Figueira et al. (2017) for detailed information regarding the experimental paradigm.

EEG recording and pre-processing

EEG data were recorded continuously from 64 active electrodes placed according to the international 10–20 system in an elastic electrode cap (BrainProducts, Munich, Germany). Data were sampled at 500 Hz using Cz as the online reference and FPz as the ground electrode.

Pre-processing steps were as follows. Continuous data were re-referenced to the average of TP9 and TP10 electrodes and digitally filtered using a second-order Butterworth high-pass filter 3 dB at 0.01 Hz (12 dB/octave). Then, we removed eye-blink artifacts using the semi-automatic Independent Component Analysis tool in BrainVision Analyzer 2.1 software. Components (maximum of two) were removed from the data only after inspection of topographical maps demonstrating their proximity to the ocular area and their resemblance to established waveform characteristics (Jung, Makeig, Humphries, et al., 2000). Epochs of 1,800 ms length were extracted from the continuous signal (600 ms pre- and 1,200 ms post-arrow cue onset). Epochs containing voltage deviations of $\pm 100 \mu V$ were rejected as well as epochs containing horizontal eye-movements. An average of 89.92% of the total trials were retained for further analyses (88.39% and 89.48% for the neutral emotional state, two and four squares, respectively; 91.06% and 90.96% for the unpleasant emotional state, two and four squares respectively).

Time-frequency analyses

The present study focused on alpha oscillations, specifically the alpha-band in the 8–12 Hz frequency range. Only artifact-free single trials with correct responses were used to investigate the temporal dynamics of alpha oscillatory activity. We used a family of complex Morlet wavelets with a Morlet parameter $m = f_0 / \sigma_{\text{freq}} = 7$, which resulted in a frequency resolution of 1.43 Hz and a time resolution of 111 ms (full width at a half maximum) at a center frequency of 10 Hz. Complex wavelets were calculated for frequencies between 3.88 and 41.67 Hz in steps of 0.55 Hz. The resulting time-by-frequency data for each time point were kept for further analyses. Time-varying amplitudes were divided from the mean of a baseline segment between 600 and 400 ms prior to arrow-cue onset.

Inter-site phase-locking analyses

To quantify systematic relations of oscillatory phase across the sensor array, at a given frequency and time, we calculated inter-site phase-locking (ISPL) values. To this end, the complex phase values obtained after wavelet transform for each

Fig. 1 Example of the sequential order of events in a trial inside a neutral block. From 2,000 to 2,100 ms of the fixation cross onset, a neutral or an unpleasant picture would appear centrally and stay on the screen for 1,000 ms. In this example, because this would be a trial inside a neutral block, a neutral picture would appear. The WM change-detection task (Vogel et al., 2004) started from 600 to 700 ms following the offset of the picture. This task began with the onset of an arrow cue for 200 ms. The arrow pointed to the left on half of the trials. The arrow cue would then be

replaced with a memory array that would stay onscreen for 100 ms. After a 900-ms retention interval (RI), a test array would follow, staying onscreen until the participant's response, for a maximum of 2,000 ms. Participants should compare the test array to the previously shown memory array and respond if a square on the previously cued hemifield changed color or not. Participants were instructed to respond as quickly as possible and try to not commit errors

trial, electrode, time point, and frequency were first normalized by dividing by the corresponding absolute value. Then, differences between a reference electrode pair (O1/O2) and the remaining electrodes were calculated, and the result normalized again, to minimize the impact of overall signal energy and of volume conduction (see McTeague, Gruss, & Keil, 2015; Nolte, Bai, Wheaton, et al., 2004). These complex values were then trial-averaged, and the absolute value (modulus) of the average taken. The resulting inter-site phase-locking values indicate to what degree the phase differences across sensors are constant across trials (Lachaux et al., 1999). Considering our focus on parieto-occipital alpha activity, the ISPL values were then averaged within the alpha-band, including wavelets with center frequencies between 9.44 and 10.55 Hz. This resulted in electrode-by-time matrices for each participant and condition, submitted to statistical analysis as described below.

Behavioral analysis

Error

Statistical analyses EGG

To fully use the temporal and spatial information of the data, the alpha power time courses for each sensor were submitted to general linear model approach and F-contrast weights computed for each time point and sensor, using permutation control for alpha error accumulation. First, we modeled three main effects: Hemisphere (Contralateral vs. Ipsilateral), Load (4 vs. 2 items) and Emotional State (Unpleasant vs. Neutral).

To control for multiple comparisons, we used an F-max reference distribution (Blair & Karniski, 1993), based on 8,000 random permutations of the data: Data were shuffled across conditions within each participant, and F-value matrices (sensor by time points) were re-calculated 8,000 times.

The maxima of these F-value matrices were used to create a distribution of F-max values for each time and frequency points. The 0.95% tail of this distribution served as the cutoff for statistical significance, and was determined separately for each comparison.

To account for possible interactions between Hemisphere, Load, and Emotional State we also included the data for all time points and scalp locations in a $2 \times 2 \times 2$ ANOVA. All F-values obtained for two-way interactions and the three-way interactions were below 8.00, and thus did not reach the threshold determined by permutation testing (see above). Therefore, we discarded the interactions between the factors.

Power values and statistical parameters were analyzed in terms of contra- and ipsilateral conditions, rather than left/right hemifield conditions, as is customary in lateralized change-detection tasks. In other words, we used the difference between hemifield conditions with same load as the dependent variable. Such a procedure is aimed at eliminating perceptual confounds produced by physical differences in the memory array. It should be noted, however, that this subtraction approach may not eliminate non-linear effects of load.

A note should be made regarding topographical maps shown in the results section: due to the subtraction procedure, we mirrored the F-values against the other hemisphere. As a consequence, all topographical plots are symmetrical.

Behavioral analysis

Reaction time: Mean response times of correct responses were submitted to a repeated-measures analysis of variance (ANOVA) that included the factors Emotional State (Unpleasant vs. Neutral) and Load (Two vs. Four Items). **Error:** Incorrect responses included anticipation (reaction time (RT) < 150 ms), slow responses (RT > 2,000 ms), and incorrect key-press responses. The total number of incorrect responses was submitted to a repeated-measures

analysis of variance (ANOVA) that included the factors Emotional State (Unpleasant vs. Neutral) and Load (Two vs. Four Items).

Results

Permutation-controlled analyses: Time-varying power

F-values exceeded the critical value only for the main effect of Hemisphere in the alpha-band, showing greater alpha reduction effect for the contralateral hemisphere in comparison to the ipsilateral hemisphere. As shown in Fig. 2, the parietal-occipital sensors P3/P4, P5/P6, P7/P8, and O1/O2 showed sustained differences (above the permutation-controlled threshold) for more than 50% of the 800–1,200 ms time-window that comprises the second half of the Retention Interval (RI). This result served as a manipulation check, replicating previous findings using lateralized cognitive tasks. The remaining main effects (Load and Emotional State) did not reach the permutation-controlled significance threshold (14.60).

Permutation-controlled analyses: Inter-site phase-locking analyses

Hemisphere effects

The F-value for the inter-site phase-locking (ISPL) data exceeded the F-value threshold (9.55) for all main effects in

the alpha-band. The Hemisphere main effect comprised only three pair of sensors (CP5/CP6, P3/P4 and P7/P8) for more than half of brief time-window of 100–180 (Fig. 3), indicating higher coupling between those sensors and the O1/O2 seed in the contralateral hemisphere.

Load and emotional state effects

Both the Load and the Emotional State main effects comprised a broad fronto-central area. The Load main effect was found in two different time-windows representing the beginning (400–550 ms) and the end (800–1,000 ms) of the retention interval. That is, we found greater inter-site phase-locking between fronto-central areas and the occipital pole (O1/O2 seed) for the four-item compared to the two-item condition during the retention interval. Figure 4 illustrates the finding of greater phase synchrony between the occipital pole (O1/O2 seed) and fronto-central areas for the four-items condition in comparison with the two-items condition.

An Emotional State main effect (Fig. 5) was also found in two different time windows, the first one (200–250 ms) representing the onset of the to-be-memorized array and the second one (850–950 ms) representing part of the retention interval. For the first one, we found greater coupling for the neutral emotional condition, suggesting that when a trial is preceded by an unpleasant picture, the top-down control exerted by frontal areas is disrupted. Surprisingly, by the end of the retention interval, we observed the opposite pattern: the unpleasant emotional state elicited greater coupling between frontal areas and the seed.

Fig. 2 Power changes for the Hemisphere main effect. **Left:** On the top (contralateral) and bottom (ipsilateral), grand means ($N = 28$) time-frequency planes showing power changes at parietal-occipital sensors P3/P4, P5/P6, P7/P8, and O1/O2, where time zero is the onset of the arrow cue. **Right:** On the top, grand mean subtraction between contra- and ipsilateral hemispheres. On the bottom, topographical map of the

permutation-controlled F values comparing power changes for the main effect of hemisphere at 900 ms. The highlighted black electrode represents the Cz and the highlighted white electrodes on the topographical map crossed the significance threshold for more than 50% of the 800- to 1,200-ms time-window. Note: the data were mirrored against the opposite hemisphere

Fig. 3 Inter-site phase-locking (ISPL) for the Hemisphere main effect. **Left:** On the top (contralateral) and bottom (ipsilateral), grand means ($N = 28$) time-frequency planes showing ISPL changes at CP5/CP6, P3/P4, and P7/P8 sensors. **Right:** On the top, grand mean subtraction between contra and ipsilateral hemispheres. On the bottom: topographical map of the permutation-controlled showing the F values for the main effect of

hemisphere at 150 ms. The highlighted black electrode represents the Cz and the highlighted white electrodes on the topographical map crossed the significance threshold (9.55) for more than 50% of the 100- to 180-ms time-window. Note: the data were mirrored against the opposite hemisphere

Behavioral results

The main effect of Load approached significance for both the Reaction Time ($F(1,27) = 77.96$, $P < 0.01$) and the Incorrect Response ($F(1,27) = 170.52$, $P < 0.01$). Participants committed more errors and were slower when the load was higher (for a descriptive analysis, see Table 1). The main effect of Emotional State did not approach significance for either Reaction Time ($F(1,27) = 2.15$, $P < 0.15$) or Incorrect Response ($F(1,27) = 0.63$, $P < 0.44$). Furthermore, the interactions between Load and Emotional State did not approach

significance for Reaction Time ($F(1,27) = 0.002$, $P < 0.96$) or Incorrect Response ($F(1,27) = 0.02$, $P < 0.90$)

Discussion

The current study investigated large-scale brain oscillatory activity in the alpha range in a lateralized change-detection task, manipulating WM load and emotional state. Specifically, we quantified parieto-occipital alpha power asymmetry and large-scale oscillatory coupling of alpha phase

Fig. 4 Inter-site phase-locking (ISPL) for the Load main effect. **Left:** On the top (four items) and bottom (two items), grand means ($N = 28$) time-frequency planes showing ISPL changes at F1/F2, F3/F4, F5/F6, F7/F8, and AF3/AF4 sensors. **Right:** On the top, grand mean subtraction between the four-items and the two-items conditions. On the bottom: topographical maps of the permutation-controlled showing the F values for the

main effect of Load at 500 ms and 900 ms. The highlighted black electrode represents the Cz and the highlighted white electrodes on the topographical map crossed the significance threshold (9.55) for more than 50% of the 400- to 550-ms (left) and 800- to 1,000-ms (right) time-window. Note: the data were mirrored against the opposite hemisphere

Fig. 5 Inter-site phase-locking (ISPL) for the main effect of emotional state. **Left panel**, top (unpleasant) and bottom (neutral), grand means ($N = 28$) time-frequency planes showing ISPL changes between occipital seed sensors and F3/F4, F7/F8, AF3/AF4, and FC3/FC4 sensors. **Right panel**, top: grand mean difference between the unpleasant and neutral conditions. On the bottom, topographical maps of the permutation-

controlled F tests for the main effect of Emotional State at 250 ms and 900 ms. The highlighted black electrode represents the Cz and the highlighted white electrodes on the topographical map crossed the significance threshold (9.55) for more than 50% of the 200- to 250-ms (left) and 850- to 950-ms (right) time-window. Note: the data were mirrored against the opposite hemisphere

across recording sites (ISPL). The results showed greater coupling between fronto-central areas and the occipital pole (O1/O2 seed) for the four-item compared to the two-item condition, and for the neutral emotional state condition compared to the unpleasant emotional state. Thus, the present findings are consistent with the hypothesis that maintaining four items (vs. two items) requires greater top-down control over the visual cortex. In addition, we also found that the interconnectivity between frontal regions and the occipital pole was modulated by the emotional state; that is, for the neutral emotional state that was a greater coupling when the first array had to be encoded in WM; however, when the unpleasant emotional state was elicited, this pattern was disturbed. On the other hand, by the end of the retention interval, the unpleasant emotional state elicited greater interconnectivity between frontal areas and the occipital pole.

As a manipulation check, the results showed greater parieto-occipital alpha reduction in the contralateral hemisphere compared to the ipsilateral hemisphere during the retention interval, replicating previous work (e.g., Sauseng et al., 2009). In addition to the time-varying power, we found greater coupling between centro-parietal sensors and the O1/

O2 seed in the contralateral compared to the ipsilateral hemisphere, during the retention interval.

Our present findings suggest that the experimental emotional modulation disrupted the typical interconnectivity between frontal and occipital areas, especially when the memory set was encoded. A rich body of studies has demonstrated that the processing of emotionally engaging stimuli is prioritized due to their evolutionary relevance (Oliveira et al., 2013; Wieser, Miskovic, & Keil, 2016). When it comes to emotion-WM interactions, it is known that storing task-irrelevant emotional stimuli can diminish the active maintenance of task-relevant information, which may indicate a competition for limited WM capacity (Dolcos & McCarthy, 2006; Stout et al., 2013). Therefore, it is conceivable that the competition between colored squares and highly motivational unpleasant pictures disrupted the top-down control exerted by the frontal cortex (cf., Dolcos & McCarthy, 2006). Unexpectedly, at the end of the retention interval, we observed greater fronto-occipital phase-locking during the unpleasant compared to the neutral condition. This unpredicted finding is consistent with earlier reports showing that interference versus facilitation effects exerted by emotional stimuli change

Table 1. Behavioral descriptive analysis

	2-Items		4-Items	
	Unpleasant	Neutral	Unpleasant	Neutral
Mean RT $\pm$ SD	693.3 $\pm$ 188.8	722.1 $\pm$ 216.7	784.1 $\pm$ 200.5	809.8 $\pm$ 207.8
Mean Error $\pm$ SD	5.3 $\pm$ 7.8	4.5 $\pm$ 7.8	16.6 $\pm$ 6.2	15.6 $\pm$ 6.2

over the course of a trial (Müller, Andersen, & Keil, 2008). Importantly, the direct effect of unpleasant picture viewing on WM capacity previously observed using the ERP methodology (Figueira et al., 2017) was not borne out when considering oscillatory power activity in the alpha-band. Thus, these two EEG measures yield complementary, unique information.

Sauseng et al. (2009) reported that the amplitude of alpha-band power increases with load during the retention interval in a change-detection task. Here, we did not replicate this Load effect for the time-varying power data, but results showed a main effect of Load on inter-site phase locking in the alpha band. The present findings thus suggest greater interconnectivity in the alpha frequency band, between frontal regions and the occipital pole, during the retention interval in the four-item versus the two-item condition. This finding is in line with results described by Palva et al., (2010) that showed strengthened synchrony among the frontoparietal regions by increasing memory load. Sadaghiani et al., (2012) demonstrated a link between global phase synchrony and frontoparietal network, using EEG-fMRI recordings. Importantly, their findings are specific for alpha activity, which highlights the importance of alpha-band coupling in a well-defined top-control network. In other words, there is strong evidence that alpha-band phase locking is involved in the regulation of attentional top-down modulation, predominantly within those specific frontoparietal and visual cortices that are known to be active during VWM processing with fMRI.

Thus, even though the alpha-band power was not influenced by the number of items held in WM (see also Jensen et al., 2002), the degree of alpha synchronization across brain regions was. This may be taken to suggest that maintaining more items in WM requires greater top-down control in comparison to fewer items. Future work may aim to clarify this relationship and to further examine the relation between number of items and the degree of synchronization.

The current finding of alpha reduction in the contralateral compared to the ipsilateral occipital cortex is in line with notions that consider hemispheric alpha power asymmetries as a consequence of inhibition in visual input. For example, Schneider et al. (2019) proposed that this asymmetry plays a role in the orienting of attention within WM. It has been suggested that alpha lateralization arises from an alpha increase in the ipsilateral cortex to mediate the inhibition of the ipsilateral task-irrelevant cortical regions (Jensen & Mazaheri, 2010). Consequently, our results point to a functional role of ipsilateral alpha enhancement in suppressing irrelevant WM representations and favoring the processing of the to-be-memorized hemifield. We also found greater interconnectivity between centro-parietal regions and the occipital pole in the contralateral hemisphere during the presentation of the arrow cue, that is, before the onset of the memory array. It is consistent with

current conceptual models of alpha oscillations that this phase adjustment in the contralateral hemisphere serves to protect WM against the items presented in the non-cued hemifield (Bonnefond & Jensen, 2012).

One limitation that might arise with the inter-site phase-locking technique is due to volume conduction, which in turn may lead to spurious connectivity estimates. To overcome this limitation, we normalized the complex phase and the complex inter-site phase differences to unit length prior to phase-averaging (Wieser et al., 2016). Future neuroimaging studies are needed to shed light on the interaction between frontal cortex and visual sensory areas during WM processing, and to trace the flow of information between those areas during cognitive tasks that engage WM resources. Furthermore, we delivered the same visual information to both hemispheres and used the difference between the electric activity on ipsilateral and contralateral hemispheres as the dependent variable, with the intention to remove linear effects due to the physical appearance of the stimuli. Studies that examine non-linear effects of set size on selective visual processing, accounting for both hemispheres, are still needed. Equally important, however, is to further clarify the neural circuits implicated in the interaction between emotion and WM.

Conclusion

Taken together, our results provide evidence for the role of alpha-band activity in the service of executive control. In this regard, frontal-occipital interconnectivity in the alpha-band could be interpreted as the mechanism that influences the way in which a stimulus is to be processed. The current findings, specially the inter-site phase-locking results, can be added to the WM and attention literature (see, e.g., Jensen & Mazaheri, 2010) that postulate alpha-band activity as being part of a control mechanism that promotes inhibitory gating of information processing. Furthermore, we provided evidence that neutral and unpleasant emotional states differentially modulate the neural correlates of relevant information encoding, contributing to a better understanding of how emotional states influence WM processing.

Open practices statement None of the data or materials for the experiments reported here are available, and none of the experiments was preregistered.

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