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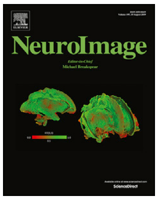

Closing eyes during auditory memory retrieval modulates alpha rhythm but does not alter tau rhythm

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ABSTRACT

The alpha power increase that occurs when the eyes are closed is one of the most well-known effects in human electrophysiology. In particular, previous psychological studies have investigated whether eye closure can boost memory performance under certain circumstances, providing contradictory evidence across sensory input modalities. Although alpha power is modulated during different phases of memory and these modulations are correlated with performance, few studies have reported on the relationship between eye closure, memory, and alpha-band power. The present study investigates the influence of eye closure while participants ($n = 21$) performed an auditory recognition memory task with spoken words during the recording of magnetoencephalography (MEG) data. Our results showed no evidence for a behavioural effect of eye closure in the performance of the task. In addition, electrophysiological responses to the stimuli showed the expected alpha event-related desynchronization (ERD) 0.5–1 s and a high-alpha/beta event-related synchronization (ERS) 1–2 s after word onset. The data showed the expected memory effect, i.e. remembered words elicited greater 10 Hz ERD than forgotten words in the brain regions typically associated with the language network, suggesting a modulation of tau rhythm. Eye closure modulated alpha rhythm only in posterior-parietal and occipital regions. The lack of interaction and the different localizations found for modulations of tau and classical alpha rhythms suggests that these rhythms play distinct functional roles in memory performance.

1. Introduction

Since alpha oscillations were first described in electroencephalographic (EEG) signals by Berger (1929) almost a century ago, thousands of studies have investigated their neurophysiological origins and relationship to cognition and brain function. The alpha rhythm occurs in the 7–13 Hz range and can be clearly detected as an increase in power in posterior sensors when the eyes are closed compared to when they are open (Berger, 1929). Source reconstructions have associated this power change with visual cortex (Barry et al., 2009, 2007). However, alpha is not the only rhythm that fluctuates in this frequency range. Previous studies have identified two other 7–13 Hz rhythms: the mu rhythm and a third rhythm (later termed tau). The mu rhythm is an oscillation present in motor-related areas, and is associated with desynchronization when participants perform motor tasks (Pfurtscheller et al., 1997). Similarly, the third or tau rhythm is found in the middle temporal region as a desynchronization when subjects listen to auditory stimuli and is thought to be independent of posterior alpha and mu rhythms (Hari, 1993; Hari et al., 1997).

The aim of the present experiment was to use MEG to study how alpha-range rhythms respond to auditory stimuli in an episodic memory task, with special attention to the role of eye closure. The observed pattern of alpha range rhythms varies across memory tasks. Beta rhythm has been found to respond to stimuli in different memory tasks along with alpha rhythm. Both alpha and beta desynchronization have been found in response to stimuli during the encoding and retrieval phases of tasks involving short-term memory (e.g. Klimesch et al., 1993), semantic memory (e.g. Doppelmayr et al., 2005) and episodic memory (e.g. Klimesch et al., 1997). Klimesch (1999) suggested that larger decreases in alpha and beta bands reflect better cognitive and memory performance. For the encoding phase, larger alpha desynchronization has been found for later remembered words compared to later forgotten words (known as the subsequent-memory effect, Klimesch et al., 1997; Hanslmayr et al., 2012). For the retrieval phase, larger alpha desynchronization has been found for better performers (i.e. the participants who remembered more words) compared to worse performers (i.e. those who remembered fewer words, Klimesch et al., 1993). Not only has this pattern been found in

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different memory tasks (for a review, see Klimesch, 1999; Hanslmayr et al., 2012; 2016), but also in other cognitive tasks such as mental rotation (Klimesch et al., 2003; Hanslmayr et al., 2005).

Moreover, the magnitude of alpha desynchronization in response to a stimulus depends on the absolute power of alpha in the pre-stimulus interval (Pfurtscheller and Aranibar, 1977). The larger the absolute alpha power in the pre-stimulus interval, the larger the alpha desynchronization in response to the stimulus. Klimesch, Sauseng and Gerloff (2003) modulated alpha power dynamics in a mental rotation task using TMS. Higher absolute alpha power during the baseline period induced greater alpha desynchronization in response to the stimuli, which resulted in better behavioural performance. Similar results were reported in Hanslmayr et al. (2005) using neuro feedback training to increase absolute alpha power in the baseline period.

An important point for the present study is the fact that all of these studies used visual stimuli, whereas similar modulation of memory retrieval has not been found in studies using auditory stimuli. For instance, Krause et al. used an auditory memory task with tones and found no evidence for the classical alpha event-related desynchronization (ERD, Krause et al., 1995). Conversely, bilateral alpha ERD was found in an auditory memory task with vowels even though no modulation due to task performance was detected (Krause et al., 1996). A possible explanation for these negative results using auditory stimuli may be that observing the 7–13 Hz (tau) rhythm has been more elusive in EEG than in MEG or intracranial recordings (Klimesch, 1999).

Moreover, despite the large volume of research on alpha's role in memory and the boost in alpha in posterior brain regions due to eye closure, the influence of eye closure on the role of alpha oscillations in the performance of memory retrieval remains relatively understudied. The role of eye closure in memory retrieval has been examined in several behavioural studies (Glenberg et al., 1998; Perfect et al., 2011, 2008; Vredeveldt, 2011; Vredeveldt et al., 2012, 2011; Wagstaff et al., 2004). These studies report on different paradigms in which eye closure and disengagement from the environment increased the number of recalled items or experiences. Glenberg et al. (1998) showed that eye closure and disengagement from the environment increased the number of recalled words and were able to rule out the possibility that social embarrassment produced this effect. Similarly, Wagstaff et al. (2004) found enhanced memory for public events when eyes were closed at recall, and Perfect et al. (2008) showed the same effect for everyday memories of both live and videotaped events. Vredeveldt (Vredeveldt, 2011; Vredeveldt et al., 2012, 2011) reviewed several studies showing that instructing individuals to close their eyes or avert their gaze from the experimenter's face significantly improved performance on a variety of cognitive tasks, particularly memory tasks. Two hypotheses have been proposed to explain these performance boosts due to eye closure. On the one hand, according to the cognitive load hypothesis, this memory improvement may result from freeing cognitive resources by closing the eyes (Perfect et al., 2011, 2008). On the other hand, the modality-specific interference hypothesis suggests that reducing visual interference by closing the eyes promotes visualization of the event and improves memory (Vredeveldt, 2011; Vredeveldt et al., 2012, 2011).

The present study used an episodic memory task, in which the retrieval phase of the task was performed in the auditory domain. This allowed participants to perform the retrieval phase with their eyes either closed or open, and also allowed us to examine the existence and role of the different rhythms in the alpha range (7–13 Hz), including the tau rhythm previously associated with auditory tasks. Therefore, the experiment aimed at investigating 1) how rhythms in the alpha range are modulated in the retrieval phase of an episodic memory task, 2) how eye closure (visual alpha modulation) interacts with these rhythms and affects task performance, and 3) whether the role of the classical alpha and tau rhythms can be disentangled or are part of the same process in auditory memory tasks. We hypothesized that eye closure would increase alpha power at baseline and this would elicit a larger ERD during the retrieval response to a word. Based on previous behavioural results, we also hypothesized that this larger alpha ERD would help improve overall performance on trials with eyes closed compared to those with eyes open.

2. Materials and methods

The study was carried out at the Basque Center on Cognition, Brain, and Language, and was approved by its institutional review board. Twenty-one native Basque-speaking, right-handed adult participants (11 male, 10 female) were recruited for this experiment. All subjects were neurologically healthy, with no hearing or reading disorders. All participants were screened for magnetic interference prior to data collection and provided informed consent (Declaration of Helsinki) before starting the experiment. Additional data from two participants was recorded: data from one participant were discarded because this participant fell asleep, and data from another were discarded because s/he did not provide behavioural responses.

2.1. *Design and materials*

The memory performance of participants was assessed using a recognition task containing nine blocks. Each block consisted of three phases: encoding (50 trials), rehearsal (5 min) and retrieval (50 trials) for a total duration of 11 min. During the encoding phase, visual words were presented on a black back-projection screen (2 s per word), and participants were instructed to read and memorize the list of 50 words silently. In the rehearsal phase they were asked to think silently about the words they had just read. Participants were instructed that as soon as they noticed they had become distracted during rehearsal, they should, start thinking about the words again. In the retrieval phase, participants listened to probe words and had to recognise words that had been present in the encoding phase by pressing a button with the right hand (25 trials were words to be remembered and 25 trials were words to be rejected). Subjects had 5 s from the onset to reject or accept a word, pressing a button with the right hand index finger to accept and the middle finger to rejec. If no response was given within that time, the next word was played. If they responded to a word, they had to wait the remaining time (until the full 5 s were over) to listen to the next word. If more than one answer was given, only the first one was used in the analyses. Each participant performed the task in two conditions. In half of the blocks, participants were instructed to perform both the rehearsal and the retrieval phases of the task with eyes closed (EC); in the other half of the blocks, they were instructed to perform both phases with eyes open (EO; see Fig. 1). The order of the EC and EO blocks was counterbalanced across participants. Participants performed the task in Basque, and the words in each list were randomly selected from a larger set of words with similar frequencies (log10(freq), mean = 1.02; std = 0.69), length (mean = 7; std = 2.06) and syllable number (mean = 4; std = 0.95). All the words were nouns that referred to concrete and imageable concepts in daily life.

After performing the task, two resting state blocks each of 2-min duration were recorded: one block with eyes closed and the other with eyes open.

2.2. *MEG data acquisition*

Data were recorded using a 306-channel Elekta Neuromag (Elekta Oy, Helsinki, Finland) located at the MEG laboratory of the Basque Center on Cognition Brain and Language. The MEG is located in a magnetically shielded room (passive shielding; Vacuumschmelz GmbH, Hanau, Germany). Participants were told to relax and find a comfortable position between blocks in order to prevent movements during data acquisition; they were also instructed to avoid head, body and eye movements during the task. Two (vertical and horizontal) EOG channels and a single bipolar ECG lead were recorded for heartbeat and eyeblink removal by means of Independent Component Analysis (ICA). A Polhemus Isotrak (Polhemus, Colchester, VM, USA) was used to record points on the head for

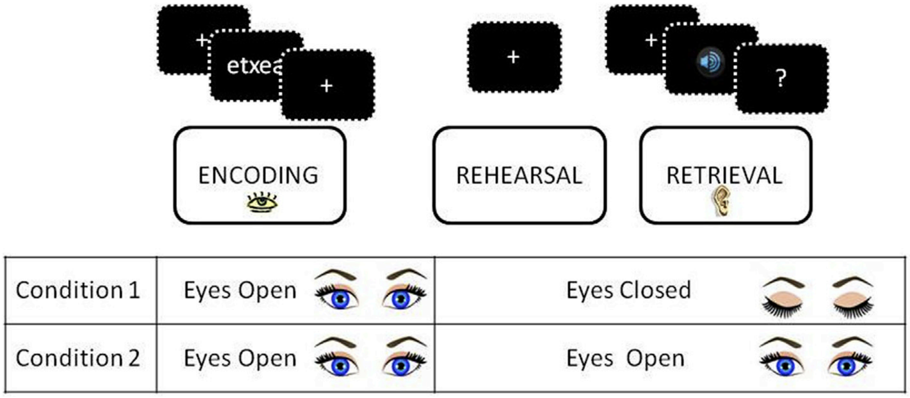

Fig. 1. Design of the experiment. The first (encoding) phase of the experiment was done with the eyes open, using visual stimuli. The second (rehearsal) and third (retrieval) phases were performed in two conditions: Eyes closed and eyes open, with auditory stimuli.

alignment of the head coordinates to each subjects structural MRI (MPRAGE, 1 mm3 voxel size). Additionally, four head localisation coils were attached to the participant's head, and their spatial location (relative to fiducials) was recorded. The four coils were active during the recordings to provide continuous head position information (cHPI). MEG data were acquired at a 1000 Hz sampling rate, high-pass filtered at 0.03 Hz and low-pass filtered at 330 Hz during acquisition.

2.3. MEG data analysis

The purpose of the first block was habituation to the task and the MEG, and these data were discarded from further analysis. Only the remaining eight blocks were used for data analysis.

2.3.1. Behavioural analysis

The proportion of trials with successful recall was modelled with a generalised linear mixed effects regression model (Dixon, 2008) with the Laplace approximation as well as posterior simulation, using eye closure as a factor (i.e. open and closed). Two models were compared: the first model included a participant random effect for the intercept ($m1 = Hit \sim Eyes + (1|Sbj)$), whereas the second model included a participant random effect for the eye closure factor ($m2 = Hit \sim Eyes + (1 + Eyes|Sbj)$).

A region of practical equivalence (ROPE, Kruschke, 2011) of one-item difference in memory recall was defined to establish if there were behavioural differences between the eyes-closed and eyes-open conditions. In other words, eye closure would be considered to have an effect on behaviour only if performance in the two conditions (eyes closed and eyes open) differed by at least one item.

2.3.2. MEG data preprocessing

Using MaxFilter 2.2, the recorded MEG data were filtered using temporal Source Space Separation (tSSS) (Taulu and Simola., 2006) with a 4-s time window and a minimum correlation of 0.98. Head origins and bad channels were supplied manually for each participant. Data were downsampled to 250 Hz, and line frequency (50 Hz) and harmonics were filtered. Following recommendations from the MEG laboratory at the MRC Cognition and Brain Sciences Unit (http://imaging.mrc-cbu.cam.ac.uk/meg/Maxfilter_V2.2), the downsampling and filtering were conducted in two separate steps.

Next, data were preprocessed using the Fieldtrip toolbox (version 20141202 (Oostenveld et al., 2011),). First, data from the retrieval period were segmented into epochs. The epochs were time locked to the onset of the word. Data were segmented into 5-s epochs consisting of 2 s before the onset of the trial and 3 s following the onset of the trial. The data were then screened for jump and other noise artefacts, padded to 12 s per trial and then filtered with a low-pass FIR filter at 40 Hz (one pass-zero phase), and the resulting epochs were normalized relative to the baseline period and detrended with respect to the whole interval. For further eye and heartbeat artefact reduction, data were decomposed using the fastICA algorithm with the number of components set equal to the number of sensors (204 gradiometers). No data dimension reduction algorithm was applied prior to ICA. Then, the correlation of each ICA component time course with the HEOG, VEOG, and ECG time courses was calculated. Components whose correlation exceeded three standard deviations from the mean correlation in any of these cases (HEOG, VEOG, or ECG) were removed before back projecting the single-trial data into the original sensor space.

2.3.3. MEG data analysis of eye-closure effect

First, alpha power modulations due to eye closure both during the resting state and retrieval phases were compared. For this analysis, the first 30 s of the resting state with eyes closed, and with eyes opened were used. In addition, the first 30 s of the retrieval phase of the first blocks with eyes closed and with eyes opened were extracted for each participant. Power values were calculated using a single Hanning taper based on frequency dependent window length. There were six cycles per time window, which was sliced in steps of 1 s. The analysis was performed on the whole epoch (30 s) between 0 and 40 Hz in steps of 1 Hz. This resulted in linearly variant frequency smoothing of 1.7 Hz at 10 Hz. Absolute power values were used for this analysis. Then, gradiometers were combined, and the statistical analyses were performed on the combined gradiometers.

A statistical analysis of alpha power was conducted to test the eye-closure effect. A randomisation distribution of cluster statistics (Maris and Oostenveld, 2007) was constructed over sensors, with power averaged across frequency and time, and used to evaluate whether there were statistically significant differences between conditions in the alpha band (7–13 Hz). In particular, t-statistics were computed for each sensor and a clustering algorithm formed groups of channels over time points based on these tests. The neighbourhood definition was based on the template for combined gradiometers of the Neuromag-306 provided by the Fieldtrip toolbox. The threshold for a data point to be included in a cluster was set at $p = 0.05$ (based on a two-sided dependent *t*-test, using probability correction), with at least two neighbours. The sum of the t-statistics in a sensor group was then used as a cluster-level statistic (i.e., the maxsum option in Fieldtrip, named clusterstat in the Results section), which was then tested using a randomisation test with 1000 runs.

2.3.4. MEG time-frequency analysis of retrieval phase

The oscillatory power of the retrieval phase was examined calculating Event Related Synchronizations (ERS) and Desynchronizations (ERD). A single Hanning taper based on frequency dependent window length (six cycles per time window) that was sliced in steps of 0.05 s was used. The analysis was performed on the whole trial (between -2 and 3 s) and between 0 and 40 Hz in steps of 1 Hz. This resulted in linearly variant frequency smoothing of 1.7 Hz at 10 Hz. Power values for each time-frequency point were normalised relative to the baseline period (−0.5, 0) s. Afterwards, gradiometers were combined, and statistical analyses were performed on the combined gradiometers in two ways:

A restricted statistical analysis was performed to test the hypothesis outlined in the introduction: alpha ERD in the retrieval phase is larger for remembered than forgotten items. Moreover, eye closure should elicit larger alpha ERD compared to the eyes-open condition. For the statistical analysis, a randomisation distribution of cluster statistics (Maris and Oostenveld, 2007) was performed in the alpha band (7–13 Hz) during the (−0.5, 2) s time window. The rest of the parameters remained the same as in the previous statistical analyses.

An unrestricted frequency analysis was performed to complement the previous analysis and check for any effects in other frequency bands that had not been considered in the hypothesis. Thus, a randomisation distribution of cluster statistics was performed on all the frequencies during the (−0.5, 2) s time window. The rest of the parameters remained the same as in the previous statistical analyses.

2.3.5. *MEG source level analysis*

Dynamic Imaging of Coherent Sources (DICS) (Gross et al., 2001) was used for source reconstruction. Structural MRI were segmented into scalp, skull, brain and CSF, and a volume conduction model was constructed based on this segmentation using a single shell approximation (Nolte, 2003) by assigning conductivity to the brain. An 8 mm grid (available in Fieldtrip) was used to construct the leadfields. Cross-spectral density matrices were calculated around 10 Hz (with a smoothing window of 3 Hz) for three time windows of interest: (0.5, 1.0), (1.0, 1.5) and (1.5, 2) s. For each time window of interest, complex spatial filters (common to the four conditions) were constructed using the leadfields and the cross-spectral density matrices of the window and the baseline (−0.5, 0) s. Afterwards, data were filtered using the common filters and the power changes relative to baseline were calculated for each condition.

For the statistical analysis, a randomisation distribution of cluster statistics (Maris and Oostenveld, 2007) was performed in each of the time windows (0.5, 1.0), (1.0, 1.5) and (1.5, 2) s. The rest of the parameters remained the same as in previous statistical analyses.

2.3.6. *Power spectrum analysis of the retrieval phase*

As a post-hoc analysis, the power spectrum of the retrieval phase of each trial (between −2 and 3 s) was computed using a single Hanning taper for a frequency range between 1 and 40 Hz. Afterwards, gradiometers were combined, and mean power spectrum was calculated for posterior occipital channels and right temporal channels separately. The peak frequency in the 7–13 Hz frequency band was calculated per subject for each condition and the grand average for each of the channel groups.

For the statistical analysis, a paired *t*-test comparing peak frequencies in occipital and right temporal channels was performed for each of the conditions and for the grand average.

3. Results

3.1. *Behavioural analysis*

The performance of the participants was on average around 0.75 for both models and did not differ across conditions. When the two models were compared, no benefit of including the participant random effect of eye closure (Pr(>Chisq) = 0.96) was found. Therefore, only the first model with a participant random effect for the intercept is reported (m1 = Hit ~ Eyes + (1 + 1|Sbj)). Based on this model, participants' proportion (95% CI) of correct trials was 0.75 (0.70, 0.79) in the eyes-closed blocks and 0.76 (0.67, 0.82) in the eyes-open blocks.

3.2. *MEG data*

3.2.1. *Eye-closure effect*

Fig. 2 displays the power difference in the alpha band (7–13 Hz) between eyes closed and eyes open for both the resting state (a) and retrieval phases (b). Although both images indicate an alpha increase in posterior sensors and have very similar topographies, the alpha power difference in the retrieval phase is smaller (see colour bars). The statistical analysis for each EC-EO comparison revealed a positive cluster for the resting state comparison (clusterstat = 343.5; p < 0.001) and another positive cluster near the significance threshold for the retrieval phase (clusterstat = 11.91; p = 0.073).

3.2.2. *Time-frequency analysis*

3.2.2.1. Restricted statistical analysis. Fig. 3 illustrates the time-frequency response to the spoken word stimulus and Fig. 4 illustrates a summary of the results of the oscillatory power analysis both at the sensor and source levels. The grand average (see Fig. 3A and Supplementary material, Figs. S1–S4) shows the expected response to a spoken word stimulus: theta ERS between 0 and 0.5 s, and alpha ERD between 0.5 and 1 s, followed by a high-alpha/beta rebound between 1 and 2 s. This was found for all conditions (eyes closed and eyes open) and items (remembered and forgotten, see Fig. 3B). The alpha ERD between 0.5 and 1 s was mainly found in left temporal and posterior occipital sensors (see Fig. 3A). The differences described below are a modulation of this pattern, revealing an ERD effect related to type of item (remembered vs. forgotten) but an ERS effect for eye closure (eyes closed vs. eyes open).

Comparing the different conditions, the data are consistent with the expected memory effect insofar as the remembered items were associated with greater alpha ERD compared to forgotten items, in both the eyes-closed and eyes-open conditions. For the eyes-closed condition, the a priori statistical analysis in the alpha band (7–13 Hz) revealed a cluster (clusterstat = −2214; p = 0.002) that lasted between 0.6 and 1.75 s (Fig. 4A, bottom row). For the eyes-open condition, a significant cluster (clusterstat = −1470; p = 0.006) was found between 0.65 and 1.65 s (see Fig. 4A, top row).

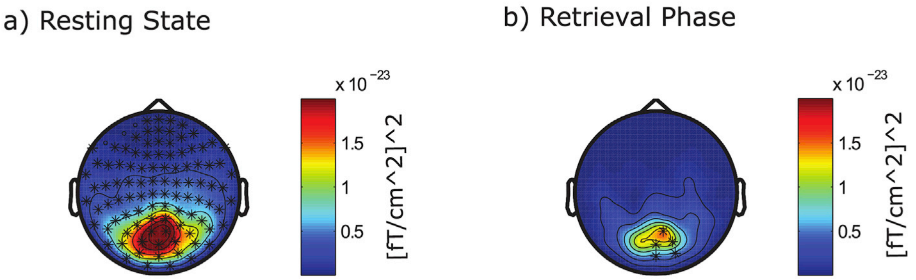

Fig. 2. Alpha band power analysis. Alpha band (7–13 Hz) absolute power difference topographic distribution between eyes closed and eyes open, for the resting state (A) and retrieval (B) phases. Warmer colours denote greater power for eyes closed, and cooler colours denote small or almost no differences. Asterisks mark the sensors that were part of the cluster resulting from the statistical analysis.

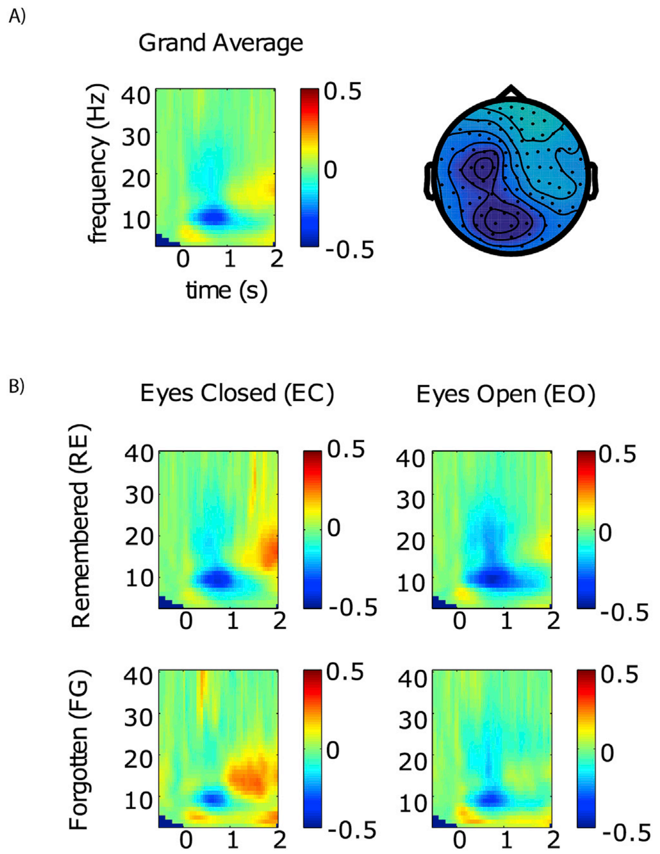

Fig. 3. A) Grand average time-frequency plot in response to spoken word stimulus and the topography of the alpha (7–13 Hz) ERD between 0.5 and 1 s. B) time-frequency plots in response to spoken word stimulus for each of the experimental conditions.

Moreover, an eye-closure effect was also found. For both types of items (remembered and forgotten) there was stronger alpha ERS between 1 and 2 s in the eyes-closed compared to the eyes-open condition. For the remembered items, a significant cluster was found between 1 and 2 s (clusterstat = 1401; $p = 0.02$) (see Fig. 4B, top row). For the forgotten items, there was also a significant cluster (clusterstat = 1714; $p = 0.002$) between 1 and 2 s (see Fig. 4B, bottom row).

For visualization of the topographies of these patterns, the effect was split into three different half-second time windows: 1) from 0.5 to 1 s (see Fig. 4, first column) where the strongest alpha ERD was present for the memory comparison; 2) from 1 to 1.5 s (see Fig. 4, second column) where the alpha ERD was still present for the memory comparison but there was also strong support for alpha ERS in the eye-closure comparison; and 3) from 1.5 to 2 s (see Fig. 4, third column) where the alpha ERS was strongly supported in the eye-closure comparison, with less strong support for the alpha ERD effect in the memory comparison.

The topography plots show that the memory effect in the initial period (from 0.5 to 1 s) appears as alpha ERD spread across almost all the sensors, but with the main focus in temporal sensors, especially right temporal sensors (see Fig. 4A, first column). The effect appears to be due to either greater ERD or less ERS for later remembered items, depending on the sensor location. As time evolves, the alpha ERD only remains on the temporal sensors of both hemispheres (see Fig. 4A, second and third columns). In contrast, the eye-closure ERS effect is mainly found at posterior and parietal sensors (see Fig. 4B). Although the topography is maintained across time, the magnitude of the effect increases in the later time intervals.

Statistical analyses were performed to test interactions. One analysis tested the modulation of eyes closed (Eyes closed vs Eyes open) on the item type effect (Remembered − Forgotten). The other analysis tested the modulation of item type (Remembered vs Forgotten) on the eyes closed effect (Eyes closed-Eyes open). Neither analysis revealed any statistically significant cluster (abs(clusterstat)$<$259; $p>0.7$).

3.2.2.2. Unrestricted statistical analysis. For the unrestricted frequency analysis, the analysis schema of the a priori analysis was maintained, but instead of focusing only on the alpha band, all frequencies from 3 to 40 Hz were included (see Supplementary material, Figs. S5–S8).

The results were similar to those for the restricted alpha band analysis: remembered items showed greater alpha ERD compared to forgotten items, for both the eyes-closed and eyes-open conditions. For the eyes-closed condition, the statistical analysis revealed one significant cluster (clusterstat = −8281; $p = 0.002$) in a 4–27 Hz band, during the 0.65–1.8 s time window (see Fig. 4A, bottom row time-frequency plot, and Supplementary material, Fig. S5). For the eyes-open condition, the analysis revealed one significant cluster (clusterstat = −7357; $p = 0.004$) in a 4–22 Hz band during a 0–2 s time window (see Fig. 4A, top row time-frequency plot, and Supplementary material, Fig. S5). Note that although the cluster spans a large time window, this is only true for the low frequencies around theta. For the rest of the frequencies, the time window approximately overlaps the time window of the eye-closure effect.

An eye-closure effect similar to that in the a priori analysis was also found, but it included a wider range of frequencies. For both types of items (remembered and forgotten), the eyes-closed condition elicited stronger alpha ERS between 0.6 and 2 s than the eyes-open condition but, in addition, the effect included beta ERS. For the remembered items, the statistical analysis supported a significant cluster (clusterstat = 14766; $p = 0.01$) between 8 and 38 Hz over the interval of 0.6–2 s (see Fig. 4B, top row time-frequency plot, and Supplementary material, Fig. S5). For the forgotten items, there was a cluster (clusterstat = 13840; $p = 0.006$) between 7 and 27 Hz, over the interval of 0.8–2 s (see Fig. 4B, bottom row time-frequency plot, and Supplementary material, Fig. S5). This analysis revealed that, in addition to the alpha band, the beta band during the retrieval phase was also modulated by eye closure. Moreover, the time windows for the memory and eye-closure effects seemed to overlap more than in the restricted analysis.

In the early phase, the memory effect was mainly found in the alpha band as greater ERD or reduced ERS for remembered items compared to forgotten items, in both the eyes-closed and eyes-open conditions. Compared to the restricted analysis, it included part of the beta band. Similar to the restricted analysis, the largest magnitude for the effect was found in right temporal sensors. On the other hand, an equivalent eye-closure effect was found in alpha and beta bands, as a greater ERS for eyes closed compared to eyes open. The effect was mainly found in posterior and right-parietal sensors.

Statistical analyses were performed to test for interactions (the same as for the a priori analysis). Similar to the restricted analysis, the results did not reveal any significant clusters (abs(clusterstat)$<$259; $p>0.71$).

3.2.3. *Source level analysis*

Fig. 4 also illustrates the results of the power analysis at the source level for each of the time windows, depicted below the corresponding topography. The grand averages for the three time windows show overall brain desynchronization in the alpha rhythm (7–13 Hz) (see also Supplementary material, Figs. S9–S11).

Comparing different conditions, the data are partially consistent with the sensor level analysis. In the first time window (0.5–1.0 s) (see Fig. 4, first column), the statistical analysis only showed differences between forgotten and remembered words for the eyes-open condition. The cluster was localized in the right posterior inferior temporal and right occipital lobes (clusterstat = −684.17; $p = 0.035$).

In the second time window (1.0, 1.5 s), the statistical analysis captured both item and eye-closure effects (see Fig. 4, second column). For the eyes-open condition, remembered words showed greater alpha ERD in the left IFG, posterior STG and angular gyrus

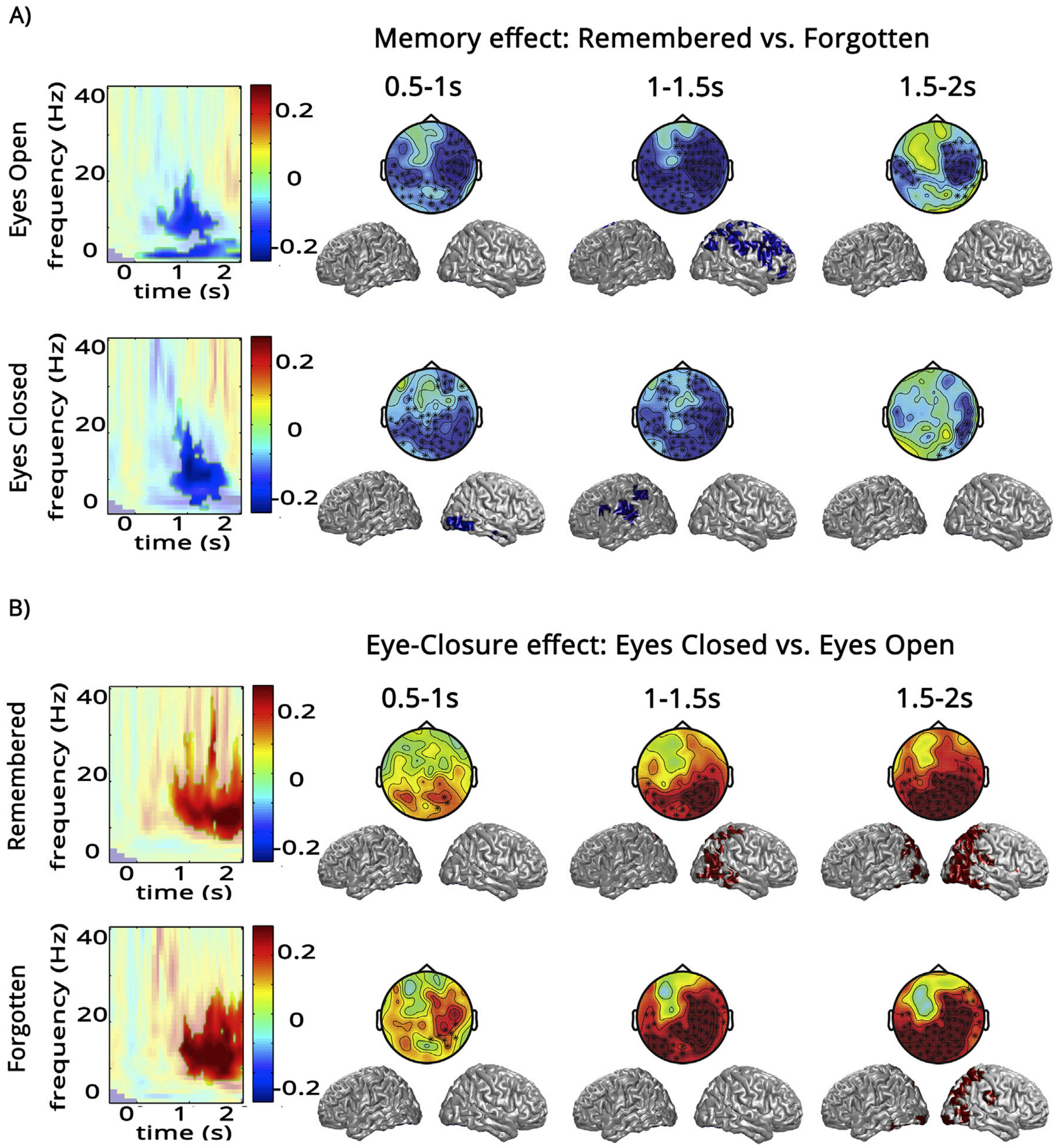

Fig. 4. Time-frequency plots, topography and source level analysis of the A) Memory effect: Remembered vs. Forgotten words for eyes open (top row) and eyes closed (bottom row) conditions. B) Eye-closure effect: Eyes closed vs. Eyes opened for both remembered (top row) and forgotten (bottom row) words. For each row, the time frequency plot in the left column shows the difference between the two conditions. Opaque colours denote statistically supported differences. The next three columns show the topography and source localization of these differences for each time window: (0.5, 1), (1, 1.5) and (1.5, 2) s, respectively. Asterisks in topography plots denote sensors that form part of the statistically significant cluster. Source localizations only show statistically significant clusters.

(clusterstat = −889.23; p = 0.017). For the eyes-closed condition, remembered words showed greater alpha ERD in the right parietal and frontal lobes (clusterstat = −1155.2; p = 0.008). For remembered words, the eyes-closed showed less alpha ERD than the eyes-open condition in the occipital and posterior-parietal lobes (clusterstat = 645.15; p = 0.049).

In the third time window (1.5, 2 s), the statistical analysis showed only an eye-closure effect (see Fig. 4, third column). Both remembered and forgotten words with eyes closed showed less alpha ERD than in the eyes-open condition, revealing two significant clusters in the occipital and posterior-parietal areas (clusterstat = 2931.1; p = 0.001 and clusterstat = 1184.5; p = 0.005).

Statistical analyses were performed to test for interactions (the same as in the previous two analyses). The results did not reveal any significant clusters (abs(clusterstat) < 222.94; p > 0.18).

3.2.4. *Power spectrum analysis of the retrieval phase*

Fig. 5 shows the mean Power Spectrums of the different channel groups (occipital and right temporal) in all the conditions. Table 1 summarizes the results of the statistical analyses of the peaks in the power spectrum, showing the mean peak frequency and standard deviation (in Hz) for each condition and channel group. The statistical analysis did not reveal any differences between the peak frequencies of right temporal and occipital channels in any of the conditions.

4. Discussion

4.1. *Summary of main findings*

In this experiment, participants recognized spoken words in a recognition memory task conducted in MEG either with their eyes open or their

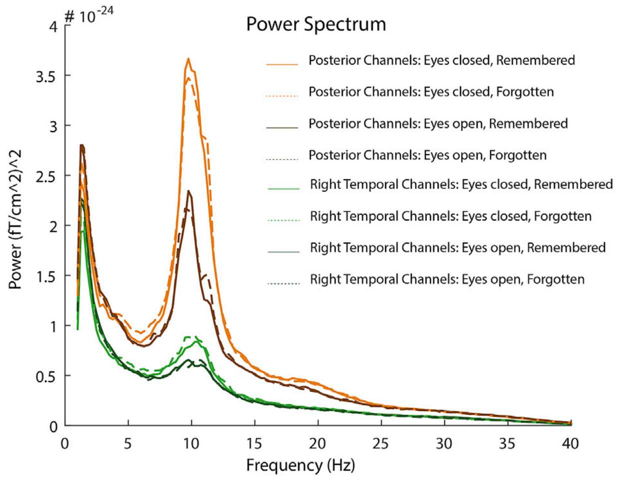

Fig. 5. Power Spectrum analysis. X axis denotes frequency (in Hz) and Y axis power (in $(fT/cm^2)^2$). Orangeish and greenish colours illustrate the power spectrum of occipital channels and right temporal channels, respectively. Lighter colours denote eyes-closed conditions, and darker colours represent eyes-open conditions. Dashed lines denote forgotten items and filled lines denote remembered items.

Table 1

Power Spectrum frequency peak analysis. First column indicates experimental condition. Second and third columns show the means (standard deviations) of the frequency peaks in right temporal channels and in posterior channels, respectively. Fourth column shows statistical results t-value(p-value) for the paired *t*-test between channel groups.

Condition	Right Temporal Channels	Occipital Channels	t (p-value)
Eyes closed, Remembered	9.44 (1.60) Hz	9.78 (1.35) Hz	−0.7616 (0.4552)
Eyes open, Remembered	9.50 (1.78) Hz	9.90 (1.44) Hz	−0.8241 (0.4196)
Eyes closed, Forgotten	9.79 (1.43) Hz	9.90 (1.37) Hz	−0.3119 (0.7584)
Eyes open, Forgotten	9.94 (1.54) Hz	9.71 (1.58) Hz	0.5795 (0.5687)
Grand Average	9.76 (1.43) Hz	9.78 (1.49) Hz	−0.0577 (0.9546)

eyes closed. Oscillatory power analysis of the MEG signals recorded in the task showed that successful memory was associated with greater alpha-band desynchronization (ERD) in the half-second interval after word presentation. Moreover, the oscillatory analysis showed two types of modulations in neuronal oscillations due to eye closure. The first was the traditional posterior alpha power increase related to eye closure, which occurs during the resting state and also, with smaller amplitude, during the retrieval phase (see Fig. 2). The second modulation due to eye closure was a modulation of power in alpha and beta bands in response to the stimuli. In both bands, the ERS effect was greater in the eyes-closed compared to the eyes-open condition at occipital and right parieto-temporal sensors. The alpha band eye-closure effect was source localised in the occipital and posterior-parietal areas, for both remembered and forgotten items. While posterior alpha modulation due to eye-closure might be expected based on the frequently observed association between eye closure and higher absolute posterior alpha power, modulation of beta power due to eye closure has not been reported to date in the literature.

No evidence of a behavioural effect due to eye closure was found. Similarly, for both alpha-ERD and high-alpha/beta-ERS, no statistical support for an interaction between eye closure and item type effects was found. Nevertheless, modulations of alpha-ERD due to item type (remembered vs. forgotten) were found in both the restricted and unrestricted analyses at similar frequency bands, time windows and sensor locations. On the other hand, the unrestricted analysis revealed an effect of eye closure with ERS modulations in both the alpha and beta frequency bands.

4.2. *Event-related responses during memory retrieval*

Previous studies have shown that during the retrieval phase of a memory task where the presented stimulus is to be categorized as new or old, alpha desynchronization occurs in response to the stimuli (Klimesch, 1999; Klimesch et al., 2003; Schack and Klimesch, 2002). Moreover, better performance has been linked to greater alpha ERD (Doppelmayr et al., 2005; Hanslmayr et al., 2005; Klimesch, 1999; Klimesch et al., 1997). Data from this experiment also demonstrated the expected memory effect: the power decrease in the alpha frequency range was larger for remembered than for forgotten items. Previous EEG studies reported an alpha modulation in electrodes consistent with posterior sources, while the effects found in this study also included MEG temporal (planar gradiometer) sensors. The source level analysis located the effect in the left superior temporal and IFG areas for the eyes-open condition. For the eyes-closed condition the effect was found in the right parietal and frontal lobes. Differences in the overall sensitivity of EEG and MEG might explain the different localization of results in the present experiment compared to results from previous studies. Alternatively, while the previously mentioned studies used visual stimuli, this study presented auditory stimuli to the participants in order to be able to study the potential effects of eye closure on retrieval. Note that Krause et al. (1996) also tested auditory memory and, even though they found bilateral alpha ERD in response to stimuli in the retrieval phase, alpha ERD was not modulated by performance.

4.3. *Tau and alpha rhythms measured by EEG and MEG*

As Klimesch (1999) suggests, the reason that the modulation of the classical alpha rhythm often seen in the visual domain is not found for the auditory domain might be because auditory stimuli instead modulate the tau rhythm in the temporal lobe. Lehtelä et al. (1997) showed that in addition to the 10 Hz parieto-occipital alpha and 10 Hz rolandic mu rhythms, there is a 10 Hz spontaneous oscillation that originates in the temporal lobe (also referred to as tau rhythm). They found that this 10 Hz tau rhythm was suppressed, especially in the right temporal area, in response to auditory stimuli, for a period starting immediately after the stimulus and lasting for about 1.5 s. Earlier, Niedermeyer (1990) reported the existence of rhythmical activity over the temporal lobes, clearly separable from the posterior alpha captured by epidural recordings but almost undetectable by scalp EEG electrodes. Moreover, this rhythm did not respond to motor activity. Later, after studying epidural recordings of a 20-year-old female in different experimental conditions such as resting, sleeping or singing, Niedermeyer (1991) named this rhythm the third or tau rhythm. The tau rhythm was most readily observed in the waking state but also persisted into drowsiness and even light sleep. During rest the tau rhythm was most pronounced in the posterior and anterior temporal lobe. As for sleep recordings, NREM sleep stage spindles were localized in the same left posterior epidural lead while the tau rhythm was localized in bilateral anterior temporal lobes. No modulation of tau rhythm was found in response to loud bang stimuli. However, the tau rhythm was desynchronized while singing a song. Based on these observations, Niedermeyer concluded that this temporal alphoid (10 Hz) rhythm was independent of the other two alphoid rhythms: posterior alpha and rolandic mu rhythms (Niedermeyer, 1991).

The tau rhythm is almost undetectable using EEG (Niedermeyer, 1997). Nonetheless, tau rhythm is detectable in epidural recordings (Niedermeyer, 1991, 1990) and also using MEG (Lehtelä et al., 1997). The experiment presented here used auditory stimuli in the retrieval phase and recorded neural data using MEG. In fact, the results showed performance-related modulation of a 10 Hz rhythm in temporal and parietal areas, an effect not yet found in the EEG literature (Klimesch, 1999; Krause et al., 1996). Bastiaansen et al. (2001) also observed different alpha ERD modulation patterns depending on recording modality. They found that preceding visual knowledge of results, ERD in the alpha range was maximal in occipital areas in both EEG and MEG recordings. However, with auditory knowledge of results, ERD in the alpha range was maximal in temporal cortex for two out of 5 participants only in MEG recordings, with no ERD found in EEG recordings. A recent study carried out using MEG showed that successful long term memory encoding was reflected in a power decrease in the alpha range in the sensory region of the to-be-attended modality (Jiang et al., 2015). The modulations were predictive of individual memory performance. Moreover, they found power increases in the alpha range in the sensory regions of the to-be-ignored modality and suggested that these increases might serve to suppress this modality.

Consequently, in agreement with Klimesch (1999), we suggest that memory experiments using auditory stimuli modulate the tau rather than the classical alpha rhythm, and therefore, MEG and/or intracranial recordings are more appropriate recording methods than scalp EEG measurements. This further suggests that the functional role of a given modulation (e.g., ERS or ERD) of a rhythm depends not only on its frequency range and time interval, but also on the specific brain network that is responsible for generating the rhythm. The role of a 10-Hz modulation of a posterior, visual cortex rhythm may not be the same as, for example, the modulation of a 10-Hz temporal, auditory cortex rhythm, even if the physiological implementation of the modulation is similar in the two cases.

4.4. *Eye closure and event-related oscillations modulation*

The eye-closure effect observed in the ERS in the beta band might be interpreted as an extension of the modulation seen in the range of the alpha band due to a broadening of the spectral peak when alpha-band power increases to include the neighbouring bands (theta and beta). Barry et al. (2007) reported a similar modulation in beta band when they studied the effect of eye closure on different frequency bands during the resting state with higher beta-band power for eyes closed in posterior and right parietal EEG electrodes. On the other hand, beta-ERS could also be explained as post-movement beta rebound (Pfurtscheller et al., 1998, 1996). After motor activity, power in the beta band of motor cortex shows ERS. In this scenario, modulation of beta-ERS would be linked to somatosensory or motor differences between conditions. A beta rebound can be modulated by different factors, for example, the force of a movement (Fry et al., 2016) or the correctness of an observed action (Koelewijn et al., 2008). To the best of our knowledge, no study has compared the beta-rebound with and without eyes-closed. However, it is plausible that making a finger movement to press a button has a different effect when the eyes are open (providing visual feedback for the movement) than when the eyes are closed (there is no visual feedback). This difference could explain the beta-band modulation seen in this experiment, although the beta-ERS modulation was mainly found in posterior sensors and not in sensors close to the motor cortices. Since the topography of the beta increase was more similar to the classic alpha eye-closure effect, as well as to the topography reported in Barry et al. (2007), we suggest that the beta-ERS modulation due to eye closure observed in this particular study was more likely to be an extension of the alpha-band eye-closure effect.

As a methodological aside, it should be noted that the comparison between eyes open and closed conditions might involve a difference in baseline power, in addition to any post-stimulus change in power. However, the greater beta-ERS seen in the eyes-closed condition is a larger relative change from a baseline that already has larger spectral power (see Fig. 2). This indicates that power differences in the eyes closed ERS are larger in absolute terms than in the eyes-open condition.

4.5. *Link between alpha and tau rhythms due to eye closure effects*

Perhaps the most striking feature of the current data is that the dynamics of the alpha/tau-band in the power responses do not show greater ERD for the response due to eye-closure, but rather a later ERS for both alpha and beta. Although our initial expectation was a classical alpha modulation due to eye closure, it is important to note that the response to an auditory word is activity related to perception and word comprehension. In contrast to the differences shown in absolute power during the resting state, our results indicate that the dynamics in different bands in response to a word, and here, to eye closure seem to relate to late ERS. Furthermore, eye closure was not associated with either a benefit or an impairment in behavioural performance. This reinforces our intuition that tau is the rhythm modulated by the memory effect in this paradigm while posterior alpha-beta is modulated by eye closure, with no direct interaction between these two modulations. Furthermore, no statistical support for a difference in the frequency peaks between the conditions in the 7–13 Hz band was found (see Fig. 5). These results are consistent with those found by Niedermeyer (1991) where the spontaneous third (i.e. tau) rhythm was not modulated by eye closure. On the other hand, the source level analysis of the data showed that eye closure modulated the localisation of the remembered vs. forgotten effect: the effect was found in the language network with eyes open, whereas it was found in the right parietal and frontal lobes with eyes closed (see Fig. 4 and Supplementary Material, Figs. S9–S11). However, no difference was found when interactions were tested statistically.

Finally, the results of the present experiment are consistent with the modality-specific interference theory, which suggests that reducing visual interference by closing the eyes promotes visualization of the event and potentially improves memory of visual stimuli, but would not help memory in other modalities (Vredeveldt et al., 2012, 2011). In this case, participants had to encode linguistic material. Recalling this material in the retrieval phase relies on the language network encompassing bilateral speech perception areas and left perysilvian language areas. Based on the oscillatory analysis results, it appears that modulating posterior alpha by closing the eyes does not directly affect processing efficiency in the language network, and as a result there was no improvement or detriment in memory performance due to eye closure in this task.

5. Conclusions

In this auditory word recognition experiment the expected memory effect was found: greater ERD in the alpha frequency range for remembered words compared to forgotten words. This effect was mainly found in temporal sensors rather than in posterior sensors. The source level analysis localized the effect in the language network and in the right parietal and frontal lobes. This is evidence that auditory or spoken linguistic stimuli modulate the tau rhythm while eye closure modulates posterior alpha. The lack of interaction between these two modulations in our experiment suggests that tau and posterior-alpha should be considered as two rhythms with distinct functional roles in memory performance. This would explain why eye closure did not enhance the memory performance of participants in this particular environment, also supporting the modality-specific interference theory for the effect of eye-closure on behavioural performance.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuroimage.2019.04.053.

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