

# Effect of Eye Closure on Anticipatory Somatosensory Alpha Oscillations

Corinne Orlemann<sup>1</sup>

**Supervisors:** Hesham ElShafei<sup>1</sup>, Saskia Haegens<sup>1,2</sup>

<sup>1</sup>*Radboud University Nijmegen, Donders Institute for Brain, Cognition and Behaviour, The Netherlands*

<sup>2</sup>*Department of Psychiatry, Columbia University, New York, USA*

Alpha oscillations (8–13 Hz) have traditionally been associated with a state of cortical idling and show an increase over posterior areas when awake participants close their eyes. In recent years, alpha oscillations have been proposed to reflect a mechanism of active functional inhibition, by suppressing cortical activity over task-irrelevant brain regions and facilitating excitability in task-relevant ones. Many studies investigated this top-down role of alpha, though it remains unclear how eye closure might impact modulation of alpha activity during cognitive tasks, and how this affects subsequent behavioural performance. In this study, we tested 33 participants performing a somatosensory spatial discrimination task in an eyes-open and closed condition, while recording brain activity using magnetoencephalography (MEG). We report an increase of alpha oscillations with eye closure and found further evidence of a functional inhibition role of alpha oscillations during somatosensory attention, reflected by alpha activity decrease over the contralateral somatosensory cortex as well as alpha increase over visual regions. Furthermore, we report the visual alpha modulation to be significantly higher for eyes-open than eyes-closed trials, implicating a necessity of increased alpha inhibition when irrelevant visual input is available. We demonstrated that this posterior anticipatory alpha activity predicted task performance, by associating higher activity with positive behavioural outcome, independent of eye condition. We therefore showed evidence that eye closure alters the general alpha activity profile and furthermore influences the anticipatory posterior alpha modulation during a somatosensory attention task. Eye closure however did not have an effect on the impact of alpha modulation on behaviour.

*Keywords: alpha rhythm, functional inhibition, eye closure, somatosensory attention, MEG*

---

Corresponding author: Corinne Orlemann; E-mail: corinneorlemann@gmail.com

Our brains continuously receive a high amount of information and are thus challenged with the task of filtering relevant input and suppressing distracting input. In recent years, cortical alpha oscillations (8-13 Hz) have been proposed to play a role in this filtering process (Jensen & Mazaheri, 2010). Furthermore, eye closure is associated with a general increase of posterior alpha (Adrian & Matthews, 1934) and is theoretically linked to facilitate sensory attentional processes by shutting out distracting visual input (Glenberg, Schroeder, & Robertson, 1998). Here, we aimed to investigate whether and how increased alpha activity due to eye closure impacts anticipatory alpha modulations during a somatosensory discrimination task.

### Inhibitory alpha

For a long time the alpha rhythm was associated with a general state of cortical idling. However, more recent research proposes that alpha oscillatory activity reflects a mechanism for functional inhibition (Klimesch, Sauseng, & Hanslmayr, & 2007; Jensen & Mazaheri, 2010; Foxe & Snyder, 2011; Haegens, N acher, Luna, Romo, & Jensen, 2011). This is supported by studies showing an increase of alpha band power over task irrelevant brain regions and networks, and a decrease of alpha power over task relevant brain regions (e.g., Pfurtscheller & Klimesch, 1991; Worden, Foxe, Wang, & Simpson, 2000; Sauseng et al., 2005). In this way, alpha oscillations are thought to gate the information flow in the brain to increase perceptual performance, which is demonstrated by an increase of alpha oscillations in anticipation of distractors (Bonfond & Jensen, 2012).

In the visual domain this targeted inhibition of task-irrelevant information occurs in a lateralized pattern (e.g., Thut, Nietzel, Brandt, & Pascual-Leone, 2006; Ikkai, Dandekar, Curtis, 2016). In other words, when a stimulus was presented in either the right or left visual field, alpha activity decreased contralateral to the attended region and increased contralateral to the to-be-ignored location (Worden et al., 2000; Sauseng et al., 2005; Rihs, Michel, & Thut, 2007; Kelly, Gomez-Ramirez, & Foxe, 2009). This alpha activity increase over occipital regions, responsible for processing the not-to-be attended visual information, is assumed to reflect an inhibition of distracting input. The pattern of lateralized alpha in- and decrease can be described by a lateralization index, defined by positive values for right-ward attention and negative values for left-ward attention (Thut et al, 2006). Importantly, the

alpha lateralization index was deterministic of target perception, with negative values preceding a more rapid and accurate detection of left-ward targets and positive-values preceding the detection of right-ward targets (Thut et al., 2006; Kelly et al., 2009; H andel, Haarmeier, & Jensen, 2011).

### Somatosensory anticipatory alpha lateralization

The lateralization pattern is not specific to the visual domain but also exists in the somatosensory domain (Haegens, Osipova, Oostenveld, & Jensen, 2010). In this case, a lateralization occurs over the right or left hemispheric somatosensory cortex, with alpha decrease contralateral to the stimulus application, indicating a similar functional mechanism for tactile tasks as the posterior alpha during visual tasks.

This lateralization pattern occurred in an anticipatory fashion prior to the presentation of an expected stimulus, when a cue guided attention towards the left or the right side. The power of this lateralization pattern furthermore decreased when this attentional cue was unreliable (Haegens, H andel, & Jensen, 2011).

Furthermore, increased somatosensory alpha lateralization modulated the subsequent task performance. For example, better performance (i.e., more accurate and faster responses) followed a higher increase of lateralized alpha over the somatosensory cortex (Haegens et al., 2011; Haegens, Luther, & Jensen, 2012). These findings show that alpha induces an anticipatory brain state of sensory regions to optimize processing in a predictive manner. Studies in the visuospatial literature indicated that lateralized alpha modulation is mainly driven by a contralateral decrease (e.g., Sauseng et al., 2005; Thut et al., 2006), while others also reported a role of ipsilateral increase (Rihs et al., 2007; Rihs, Michel, & Thut, 2009). Here, ipsilateral increase seemed especially dependent on distractor strength. Also for the somatosensory domain, ipsilateral alpha increased with the presentation of distractors, though with further increase of distractor strength a global decrease of alpha was shown both contra- as well as ipsilateral (Haegens et al. 2012). Similar to the visual information processing, somatosensory alpha therefore increased over the task-irrelevant sensory cortex, showing an inhibitory mechanism in the context of expected irrelevant information in the form of distractors.

Importantly, during somatosensory discrimination processing the lateralized alpha pattern

is accompanied by an increase of anticipatory posterior alpha power (Haegens et al., 2012). As somatosensory alpha increase is associated with an inhibition of processing of the task-irrelevant hand, the posterior alpha is assumed to reflect a general inhibition of visual input. Furthermore, posterior alpha increase also reflected a modulation on task performance, with more accurate responses emerging after a higher increase of posterior alpha (Haegens et al., 2012).

## Eye closure effect

Since the discovery of cortical alpha oscillatory activity by Hans Berger (1929) almost a century ago, it has been known that a general increase of alpha power occurs when awake participants close their eyes. This modulation is especially localized in parieto-occipital regions (Adrian & Matthews, 1934), but has also been observed in a more widespread distribution (Geller et al., 2014). However, little is known about how this general alpha effect might interact with the inhibitory role of alpha during cognitive tasks and whether these alpha activities might originate from the same underlying sources.

Anecdotally, eye closure enhances the concentration on other sensory modalities to improve the cognitive performance by suppressing visual input. This line of thought stems from the assumption of a dominant role of visual processing. In this sense, a functional imaging study reported a shift of processing networks, highlighting the exclusion of the dominant visual mode as a consequence of eye closure (Brodoehl, Klingner, & Witte, 2015). On the somatosensory level, eye closure lead to a more sensitive somatosensory threshold during a simple perception paradigm (Brodoehl, Klingner, Stieglitz, & Witte, 2015). In the context of memory recall, eye closure also facilitated recollection (e.g., Vredeveldt, Baddeley, & Hitch, 2012; Vredeveldt et al., 2015).

So far, a possible eye closure effect on the inhibitory modulation of alpha has only been investigated in the context of auditory attention (Wöstmann, Schmitt, & Obleser, 2019). The prior reported effects of lateralized and posterior alpha modulation during somatosensory attention tasks exist also for the auditory domain, showing alpha modulations for auditory spatial tasks (Banerjee, Snyder, Molholm, & Foxe, 2011) as well as for listening tasks including speech perception (Strauß, Wöstmann, & Obleser, 2014; Dimitrijevic, Smith, Kadis, & Moore, 2017). In the same manner as for the other two modalities, alpha increase over task-

irrelevant and decrease over task-relevant temporal regions improved performance during an auditory task (Dimitrijevic et al., 2017). In their study, Wöstmann and colleagues (2019) reported that eye closure not only increased the general power of alpha oscillations, but also the modulation of alpha during the attentional task. The study presented two auditory streams of numbers, which either had to be attended or ignored. In this regard, alpha activity over parietal and occipital regions increased with the presentation of the attended numbers compared to the ignored numbers, which was shown for both the eyes open as well as the eyes closed condition. Yet, this modulation of alpha significantly increased with eye closure. However, eye closure did not facilitate task performance, indicating a general neural effect of eye closure with no impact on behaviour. So far the eye closure alpha effect has not been investigated in the context of somatosensory alpha lateralization.

## Current Study

Here we aimed to investigate whether eye closure affects alpha modulation during a somatosensory discrimination task. We adapted the paradigm used by Haegens et al. (2011) to include eyes-open and eyes-closed conditions.

First, we examined differences in alpha activation for open and closed eyes, expecting higher alpha power for the eyes closed condition. Next, we analysed the pre-stimulus time window regarding the alpha activation pattern of paying attention to the left or the right hand. This pattern was further examined on a possible difference in activity based on eye closure. Lastly, we investigated whether performance was modulated by alpha lateralization and/or posterior alpha power, hypothesizing a possible effect of eye closure on this modulation.

## Method

### Participants

34 participants (Age:  $M = 25$ ,  $SD = 3.86$ , range = 20-33 years; 18 female, 16 male; 30 right handed, 2 left handed, 2 ambidextrous) took part in the experiment. One subject was excluded from analysis due to poor data quality. All participants were recruited with the online system SONA and were healthy, free from any neurological or psychiatric disorders, and reported normal hearing and normal or corrected-to-normal vision. Prior to the experiment, participants received a detailed overview of the MEG system and the study and

signed an informed consent form. The study falls under the general ethics approval (CMO 2014/288 “Imaging Human Cognition”) in accordance with the Declaration of Helsinki.

## Materials

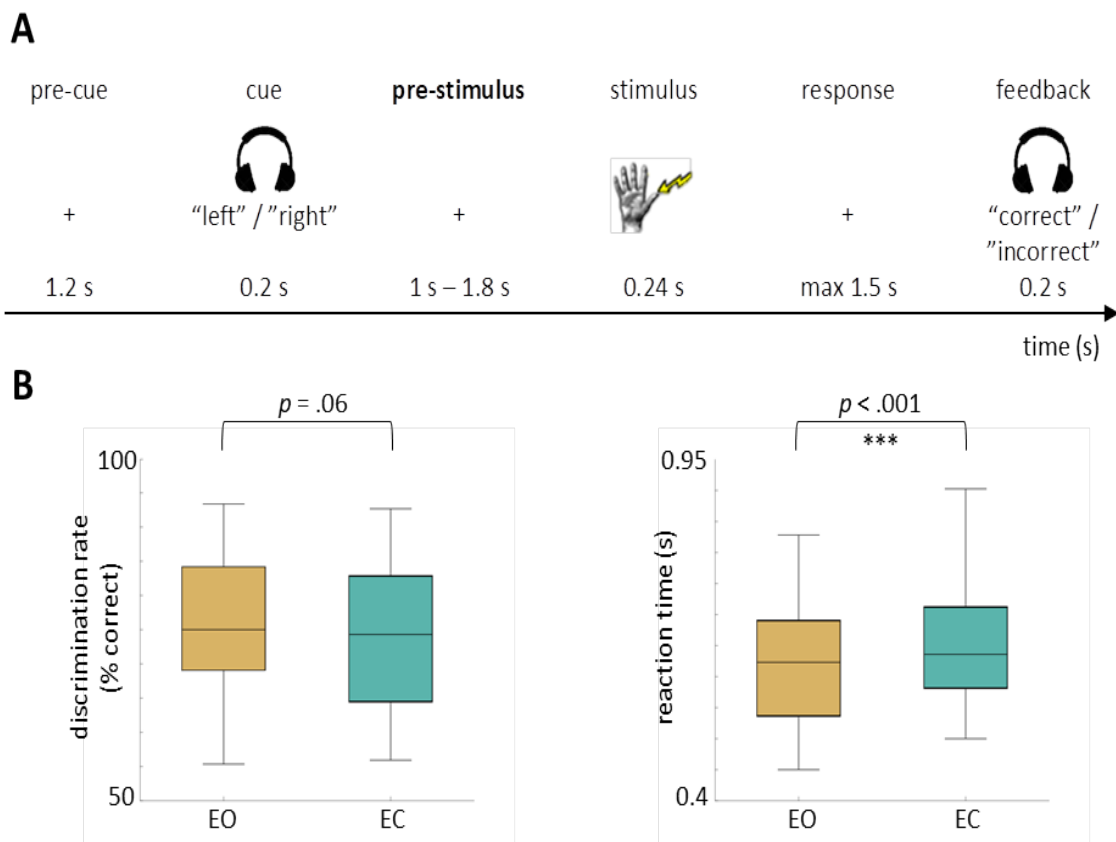
For the presentation of the sensory stimuli, two electrodes were attached to the participant’s right and left thumb. These electrodes administered a short electrical stimulus (0.2 ms) in the form of a pulse train. Electrical stimuli were generated using two constant-current high voltage stimulators (Digitimer Ltd, Model DS7A). Through the use of two Digitimer stimulators we were able to present different intensities for each hand, in order to account for the variance of sensory thresholds between hands.

Intensity of the electrical stimuli were determined by acquiring the sensory threshold for each thumb and setting the final stimulus at 150% of this threshold level ( $M_{\text{right}} = 6.4$  mA, range = 3.9 – 9.5 mA;  $M_{\text{left}} = 5.5$  mA, range = 3.2 – 9.9 mA).

During the experiment the pulse trains were presented in a low and high frequency (frequency represented by the number of pulses). Low (either 25 or 33.3 Hz) and high frequencies (41.7, 50, or 66.7 Hz) were determined for each participant individually to ensure a successful execution of the task, avoiding chance level as well as ceiling performance. Auditory cues and feedback (200 ms length each) were computer generated and presented binaurally through air-conducting tubes.

## Experimental paradigm

Participants performed a somatosensory discrimination task while their brain activity was recorded using MEG. Participants received an electrical stimulus of a low or high frequency to either the right or left thumb. Prior to the stimulus presentation, a 100% valid auditory cue guided participants’ attention to either the right or left side. Participants were instructed to determine as fast and accurately as possible whether the perceived stimulus was of the low or the high frequency. Answers were



**Figure 1.** Experimental design and behavioural results. **A.** Typical trial procedure. Participants performed the task in an eyes-open and an eyes-closed condition. The pre-stimulus interval served as the primary window of interest. **B.** Behavioural performance of the discrimination rate (left) and the RTs (right) divided into the two eye conditions. RTs were calculated only on correct trials and showed a significant difference between eyes open and eyes closed.

given via button press with the right index finger (i.e., left button press indicated the low frequency; right button press indicated the high frequency).

A typical trial started with a pre-cue interval of 1.2 s followed by the auditory cue, a jittered 1–1.8 s pre-stimulus interval, the stimulus (240 ms pulse train), a maximum response time of 1.5 s, and finally auditory feedback indicating whether the answer was correct or incorrect (Fig. 1A).

Participants performed this task under two conditions, an eyes-open condition (EO) and an eyes-closed condition (EC). Conditions were presented in a counter-balanced block-design of four blocks per condition with 76 trials each, resulting in a total of 304 trials per condition. During the EO condition participants were instructed to fixate on a fixation cross in the middle of the screen. For the EC condition participants kept their eyes closed for the duration of the block. After each block, participants were presented with a short questionnaire of four answer possibilities to rate their sleepiness (very sleepy, sleepy, awake, very awake).

Prior to the experiment, participants performed four training blocks (two per condition, 12 trials per block), during which they got familiar with the task.

Participants were seated upright in the MEG helmet and instructed to keep their head position as stable as possible for the duration of the experiment. After each block participants were able to take a short break for which they stayed seated in the MEG chair.

## Data acquisition

Whole-head brain activity was recorded with a 275-channel CTF MEG system with axial gradiometers at a sampling rate of 1200 Hz (CTF MEG Systems, VSM MedTech Ltd.). The MEG system was positioned in a magnetically shielded room. For a real time representation of the participant's head position, three head localization coils were placed at the right and left ear canals as well as at the nasion. The real time representation of the head position allowed for monitoring of head movements and adjustments to the original position. The three points furthermore served as offline anatomical landmarks. During the experiment eye movement of the left eye was tracked using an Eyelink 1000 eyetracker (SR Research Ltd.). Experimental stimuli were programmed and presented with the software Presentation (Version 18.0, Neurobehavioral Systems, Inc., Berkeley, CA, www.neurobs.com).

In a separate session an anatomical MRI of the

participant's brain was acquired, unless a recent anatomical MRI could be obtained from the database of the institute. MR images were acquired with any of the three available scanners at the Donders Centre of Neuroimaging; The 3T Siemens Magnetom Prisma MR scanner, the 3T Siemens Magnetom PrismaFit MR scanner, or the 3T Siemens Magnetom Skyra MR scanner (Erlangen, Germany). For the MRI scan participants were wearing ear plugs with drops of Vitamin E for improved co-registration of the MRIs and MEG data. The anatomical images served the purpose of source reconstruction of the MEG data; however, note that source reconstruction analysis is not included for this report.

## Behavioural analysis

For the behavioural data, we analysed discrimination rate (percentage of correct responses) and reaction times (RTs) of correct trials. A repeated-measures two-way ANOVA was computed for each of these behavioural measures with the factors eye condition (EO and EC) and cue condition (left and right).

## Pre-processing

A pre-processing pipeline for the MEG data was developed using the Matlab toolbox FieldTrip (Oostenveld, Fries, Maris, & Schoffelen, 2011). Raw data was downsampled offline to 300 Hz and epoched (-4 – 3 s, relative to the somatosensory stimulus onset). Trials were first visually inspected and rejected based on a trial summary representation of variance. Furthermore, the resulting trials were manually inspected on a trial-by-trial basis and rejected on the basis of muscle artefacts and SQUID sensor jumps. We used independent component analysis to correct for cardiac and eye movement components ( $Mean_{removed} = 8$ ). A last visual inspection of the corrected trials was performed based on variance, range, z-scores and maximum absolute values. This cleaning process was done blind to experimental condition. On average 11% of all trials were rejected during this procedure. Time window descriptions in the following analyses are always in regard to the stimulus onset as time  $t = 0$  s, unless indicated otherwise.

## Spectral analysis

Since data was collected with axial gradiometers, a transformation towards a planar representation of the MEG field distribution was calculated using

the nearest-neighbour method. Planar gradient representations allow for a clearer presentation of the data as activity is typically maximal above a source. We computed spectral representations for three time windows: the pre-stimulus window (-1 – 0 s), the post-stimulus window (0 – 1 s), and the pre-cue window (-1 – 0 s of cue-onset). The pre-cue window served as a baseline and was determined by re-defining the data to centre of the cue onset. The post-stimulus time window was specifically used for the determination of the visual regions of interest (as explained below). Fast Fourier transformations were computed for all sensors by segmenting trials into the respective time windows and multiplying them with a Hanning taper. The computation of power distributions ranged from 1 to 30 Hz.

For a time-resolved-representation of the spectral power distribution, we computed an additional time-frequency analysis (TFR) on the pre-stimulus interval (-1.5 – 0.5 s). For this, we chose a constant sliding time window of 0.5 s for each frequency (1 – 30 Hz).

### Impact of eye closure on oscillatory activity

To statistically test for power differences between the EO and the EC condition in the alpha and beta range, we computed a cluster-based permutation test on the whole head in the pre-stimulus time-window -1 s to 0 s (Maris & Oostenveld, 2007). For this test the contrast EO – EC was chosen, which leads to positive values for a stronger activation in the EO condition and negative values for stronger activation in the EC condition. This statistical analysis allows dealing with the multiple comparison problem by computing a dependent-samples t-value for each sample-pair (i.e., sensor-frequency-pairs). Samples that exceeded a p-value threshold of .05 were clustered based on their spatial adjacency. Individual cluster statistics were calculated through the summation of t-values within each cluster. Subsequently, the maximum cluster was selected as the test-statistic. Data was randomized across the two conditions and the test-statistic was repeated 1000 times. This allows to obtain a reference distribution of maximum cluster t-values to evaluate the statistic of the actual data.

### Alpha peak selection

For the sensor-level analysis, we computed the individual alpha peaks for each participant. These

peaks were selected based only on the activity in the individual visual ROIs. The FFT of the pre-stimulus interval (-1 – 0 s) was divided into EO and EC trials. We determined participants' peak frequencies by calculating the maximal absolute activity within a broad alpha range (7 – 14 Hz). As intra-individual alpha peaks did not significantly vary between conditions ( $t(32) = 0.53, p = .6$ ) they were averaged for each participant ( $M = 10$  Hz, range = 8.5 – 11.5 Hz) across EO and EC conditions.

Calculating the individual alpha peak frequencies allows taking into account the inter-individual variability of alpha frequencies between subjects. In this way, we obtained a more accurate estimation of alpha activity by avoiding a possible bias against some participants and contamination of neighbouring frequency bands, as can be the case by choosing a fixed frequency band (Haegens et al., 2014). All further analysis was computed using these individual alpha peaks unless indicated otherwise.

### Regions of interest selection

Three regions of interest (ROIs) were selected for further sensor-level analysis: A visual ROI, a left somatosensory ROI and a right somatosensory ROI. We computed these ROIs individually for each participant.

For the selection of the somatosensory ROIs, individual post-stimulus event-related fields (ERFs) were calculated regardless of eye-condition. These ERFs were divided in right-hand-stimulus and left-hand-stimulus trials. A baseline correction was applied based on the baseline window -1.5 to -1 s. The sensors with the maximum activity of the stimulus ERF determined the left and right somatosensory regions of interest.

As the experiment did not include the presentation of strong visual stimuli, the visual sensors were selected with the previously computed post-stimulus FFT (0 s – 1 s). The post-stimulus FFT was divided into EO and EC trials, averaged over trials within the two conditions, and finally contrasted in the form of EO – EC. The sensors with the maximal difference within this contrast were used for the visual ROI.

Therefore, for each participant the individual 20 maximum channels for left somatosensory, right somatosensory and visual cortex were available for further analysis.

### Alpha lateralization index

The alpha lateralization index describes the ratio

of alpha distribution over both the ipsilateral and contralateral hemispheres of the somatosensory cortex. This index is calculated based on the activity of individual alpha peaks within individual somatosensory ROIs in the following way: Alpha lateralization index = (alpha-ipsilateral – alpha-contralateral) / (alpha-ipsilateral + alpha-contralateral). The index gives positive values if alpha power activity is higher over the ipsilateral hemisphere and/or lower over the contralateral hemisphere. Negative values arise if alpha power activity is lower over the ipsilateral hemisphere and/or higher over the contralateral hemisphere. The calculation of the alpha lateralization index follows the same rationale as the index used by Thut et al. (2006).

### Effect of alpha modulation on performance

To investigate the impact of pre-stimulus alpha modulation on behavioural performance, we conducted an analysis on the alpha lateralization index as well as the visual alpha power and their interaction with the discrimination rate (percentage correct) and reaction times.

For each participant the pre-stimulus FFT (-1 – 0 s) was divided into correct and incorrect trials (omitting no-response trials) for each of the two eye conditions separately. The alpha lateralization index was computed for correct and incorrect trials for each condition following the strategy as explained above. For statistical analysis, we calculated a repeated-measures two-way ANOVA with the factors eye condition (EO or EC) and discrimination rate (correct or incorrect).

We followed the same procedure for the computation of alpha lateralization indices for fast and slow trials. For each participant, a median split of the reaction times of only the correct trials determined the categorisation of fast and slow trials. Similar to the analysis of the discrimination rate, a repeated-measures two-way ANOVA with factors eye condition (EO or EC) and reaction times (fast or slow) was computed for statistical analysis.

We repeated this process for investigating the relationship between visual alpha power and behavioural performance. The pre-stimulus FFT (-1 – 0 s) was divided into the two separate eye conditions and baseline corrected based on the baseline FFT (-1 – 0 s cue-onset, separate for each condition). The visual alpha power was computed based on individual visual ROIs and individual alpha

peaks for correct and incorrect trials, as well as for fast and slow trials. We calculated two repeated-measures two-way ANOVAs, one with the factors eye condition and discrimination rate, and one with the factors eye condition and reaction times.

## Results

Performance over all 33 participants for both eye conditions combined was an average discrimination rate of 73.4% ( $SD = 10.2\%$ ) and an average reaction time (correct trials only) of 673.1 ms ( $SD = 92.9$  ms). Figure 1B shows the discrimination rates and RTs for the EO and the EC condition.

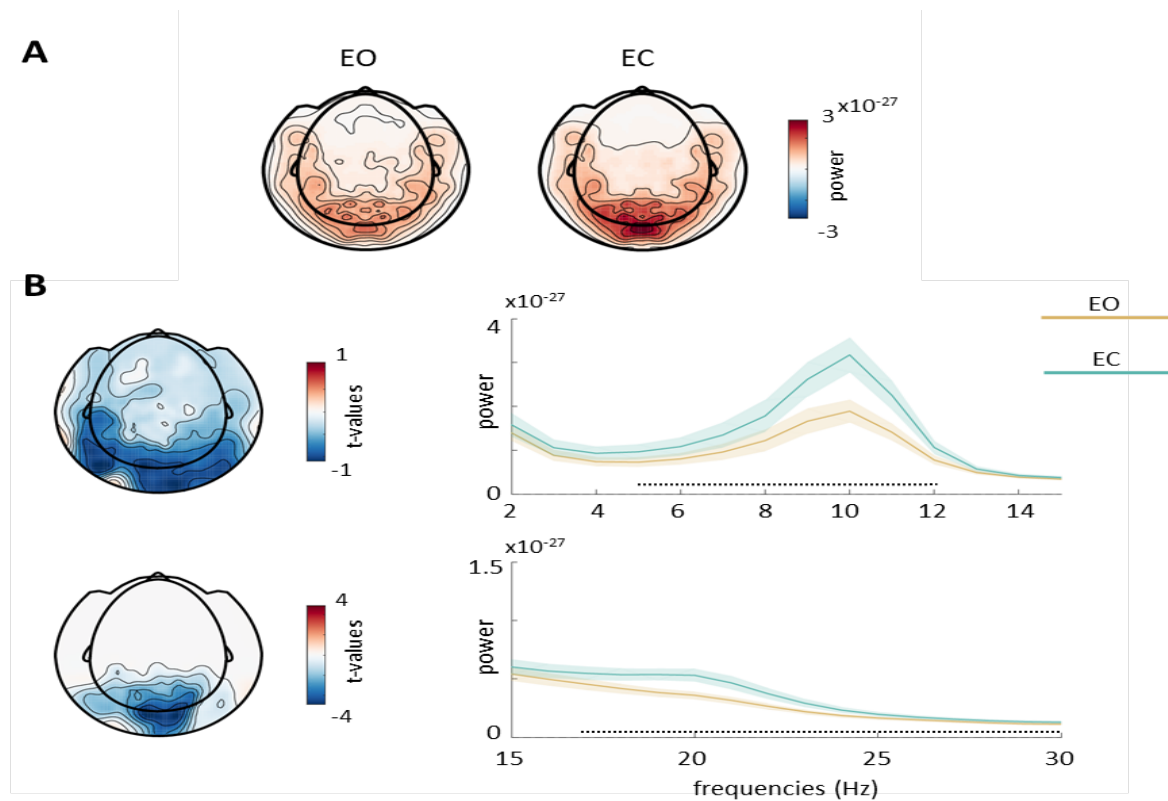
### Slower performance with eye closure

To test for statistical differences between the conditions, we calculated a repeated-measures two-way ANOVA with the factors eye (EO or EC) and attention condition (left or right) on the discrimination rate. Only a trend was observed for the main effect of eye condition ( $F(1, 32) = 3.62$ ,  $p = .06$ ), indicating higher accuracy for the EO condition. Neither the difference of attention sides ( $F(1, 32) = 0.04$ ,  $p = .85$ ), nor the interaction of eye and attention condition ( $F(1, 32) = 0.22$ ,  $p = .64$ ) were significant.

In the same fashion, a repeated-measures two-way ANOVA was computed on the RTs. The main effect of eye condition was significant ( $F(1, 32) = 31.58$ ,  $p < .001$ ) with faster performance in the EO condition. A main effect of attention side was found as well ( $F(1, 32) = 5.89$ ,  $p = .02$ ), reflecting faster RTs for the right side. This result can be attributed to the fact that participants were giving their answers through button press with the right index finger. Therefore, participants performed the task faster when the stimulus was applied to the same hand they were giving their answer with. The interaction between eye and attention condition was not significant for the RTs ( $F(1, 32) = 0.19$ ,  $p = .67$ ).

### Eye closure increases oscillatory alpha activity

Generally, the EC condition showed higher alpha and beta power in the pre-stimulus window than the EO condition, with a focus on occipital regions (see Fig. 2A). A cluster-based permutation test was computed to test the difference of oscillatory activity between EO and EC for significance. Contrasting the EO with the EC condition revealed two negative



**Figure 2.** Spectral condition differences. **A.** Non-baseline corrected FFT (1 – 30 Hz) of the pre-stimulus window ( $t = -1 - 0$  s) for eyes open and eyes closed. **B.** Cluster statistics of the EO – EC contrast. **Left:** Topographic representations of cluster distributions. **Right:** Frequency distributions of clusters, dotted lines represent frequencies with significant differences between conditions. **Top:** Widespread alpha cluster with significant frequency differences 5 – 12 Hz. **Bottom:** Occipital centred beta cluster with significant frequency differences 17 – 30 Hz.

clusters ( $p < .001$ ; Fig. 2B), one in the alpha range (7 – 14 Hz) and one in the beta range (15 – 30 Hz). The alpha cluster was distributed over widespread regions with a peak at 10 Hz, while the beta cluster was concentrated towards occipital sensors, showing the highest difference between conditions around 20 Hz. Therefore, power of both, alpha and beta oscillations, significantly increased with eyes closure.

### Anticipatory posterior alpha modulation stronger for open eyes

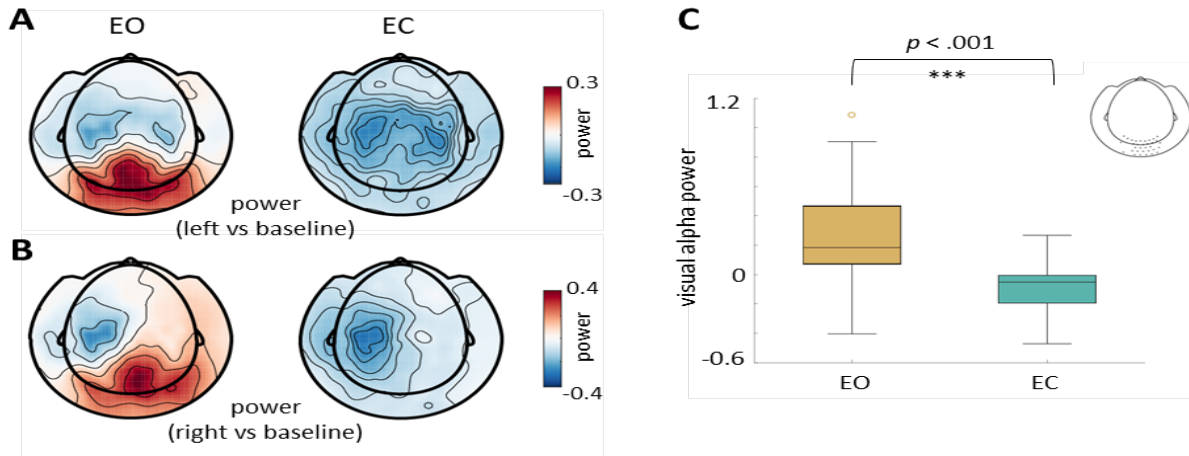
To investigate the alpha modulation during the pre-stimulus interval, we computed spectral representations of the attention conditions, by contrasting the pre-stimulus alpha activation against a baseline (i.e., left-ward attention vs baseline, right-ward attention vs baseline; see Fig. 3A & B). Only for the EO condition an increase of occipital alpha power can be observed, while both conditions show a decrease of alpha power over contralateral central sensors in anticipation of the stimulus. A paired-samples t-test was calculated on the pre-stimulus visual alpha power increase against baseline

between the two conditions to test for differences in posterior alpha modulation due to eye closure. Visual alpha power was based on individual alpha peaks and individual visual ROI sensors. The EO condition had a significantly higher posterior alpha modulation than the EC condition ( $t(32) = 6.28$ ,  $p < .001$ ; see Fig. 3C). This result reflects an increase of posterior alpha power during the pre-stimulus interval vs baseline in the eyes open condition, while the EC condition does not show such modulation. Hence, despite an overall increase of alpha power with eyes closure, the anticipatory posterior alpha modulation during the pre-stimulus interval was higher for open eyes.

### No difference of alpha lateralization between eye conditions

To further investigate the alpha power decrease during the pre-stimulus interval over contralateral somatosensory regions, we computed a normalization which takes into account leftward and rightward attention and lead to a visualisation of the previously reported lateralization pattern



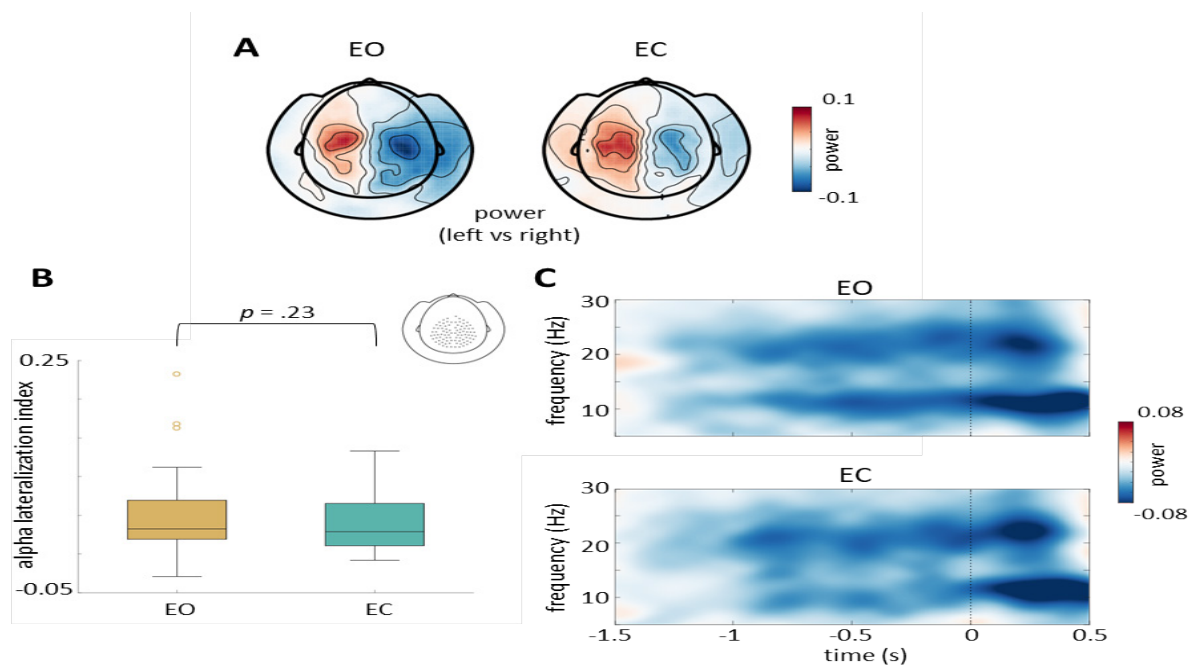


**Figure 3.** Attention modulation. Topographic plots of pre-stimulus alpha power (individual alpha peaks) modulation following the left cue **(A)** and the right cue **(B)** against baseline activity. **Left:** eyes open condition. **Right:** eyes closed condition. Both conditions show central alpha modulation based on cue direction. Only eyes open condition shows an additional modulation of visual alpha increase. **C.** Difference of visual alpha modulation between conditions ( $p < .001$ ). The empty helmet layout marks the visual ROIs used for the power estimation (summary individual visual ROIs).

(see Fig. 4A; Haegens et al., 2011; Haegens et al., 2012). We further examined the time course of this modulation of the somatosensory anticipatory alpha through the computation of time-frequency representations (TFRs). These TFRs were computed separately for the EO and EC condition in regard to the activation of lower band frequencies (5 – 30 Hz) for the left vs right normalization (see Fig. 4C; right

hemispheric sensors were mirrored to combine with left hemispheric ones). Through this visualisation we observed a sustained modulation for alpha (around 10 Hz) as well as for beta (around 20 Hz) during the pre-stimulus interval.

To investigate differences between EO and EC alpha lateralization, the alpha lateralization index over somatosensory sensors was computed for both



**Figure 4.** Left vs right attention modulation. **A.** Topographic representation of the attention left vs attention right alpha power modulation (individual alpha peaks) for the eyes open (left) and the eyes closed (right) condition. **B.** Difference of alpha lateralization index between conditions regarding the individual somatosensory ROIs represented in the empty helmet. **C.** Time-frequency representation of the low frequency (5 – 30 Hz) modulation during the pre-stimulus interval (individual somatosensory ROIs). **Top:** Eyes open condition. **Bottom:** Eyes closed condition.

conditions. There was no significant difference of alpha lateralization between the conditions ( $t(32) = 1.21, p = .23$ ; Fig. 4B). This indicates that eye closure did not have an impact on the anticipatory lateralized alpha modulation.

### No performance modulation by alpha lateralization index

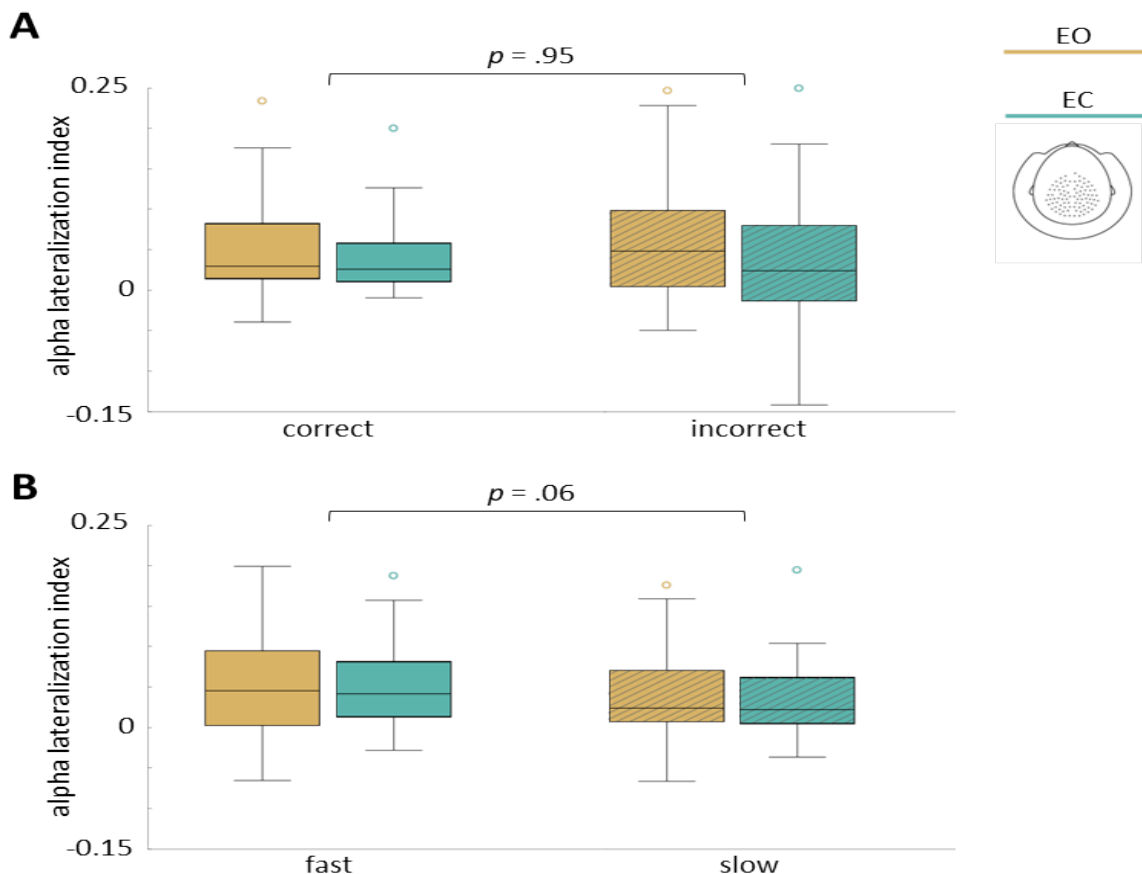
To investigate whether performance was modulated by the pre-stimulus lateralized alpha activation, we computed repeated-measure two-way ANOVAs on the lateralization index; one with the factors eye condition (EO or EC) and discrimination rate (correct or incorrect), and one with the factors eye condition (EO or EC) and reaction times (slow or fast). Figure 5 shows a representation of the results. For discrimination rate, neither the main effect of performance ( $F(1, 32) = 0.004, p = .95$ ), nor the main effect of eye condition ( $F(1, 32) = 2.77, p = .11$ ), nor the interaction ( $F(1, 32) =$

$0.7, p = .41$ ) showed significant results. Therefore, no increased alpha lateralization was found for improved discrimination for either condition.

For reaction times, no significant effects for the main effect of eye condition ( $F(1, 32) = 0.33, p = .57$ ) and the interaction effect of eye condition and RTs ( $F(1, 32) = 0.01, p = .94$ ) were found. However, a trend for the main effect of RTs ( $F(1, 32) = 3.95, p = .06$ ) can be observed, indicating a link between faster RTs and increased alpha lateralization index.

### Improved performance with increased posterior alpha power

Similar to the analysis of the lateralization index, we wanted to test for a possible influence of posterior alpha modulation on performance outcome. Therefore, repeated-measures two-way ANOVAs were calculated on the pre-stimulus posterior alpha modulation (i.e., power vs baseline) with the factors eye condition and discrimination



**Figure 5.** Behavioural performance modulation by alpha lateralization index. The empty helmet represents the somatosensory ROIs used for this analysis (summary of individual ROIs). P-values represent the main effect of performance. **A.** Modulation by alpha lateralization index on discrimination rate (% correct responses). No significant differences between correct and incorrect trials were found for either the eyes open or the eyes closed condition. **B.** Modulation by alpha lateralization index on RTs of correct trials. A significance tendency of reaction times was found, indicating a possible positive impact of increased alpha lateralization index on performance speed independent of eye condition.

rate, and the factors eye condition and RTs (Fig. 6).

For discrimination rate, a main effect of performance ( $F(1, 32) = 7.28, p < .01$ ) was found, indicating increased accuracy with higher posterior alpha modulation. A main effect of eye condition ( $F(1, 32) = 42.24, p > .001$ ) was found as well, with higher posterior alpha modulation for the EO condition. The interaction of eye condition and performance did not prove to be significant ( $F(1, 32) = 0.28, p = .6$ ).

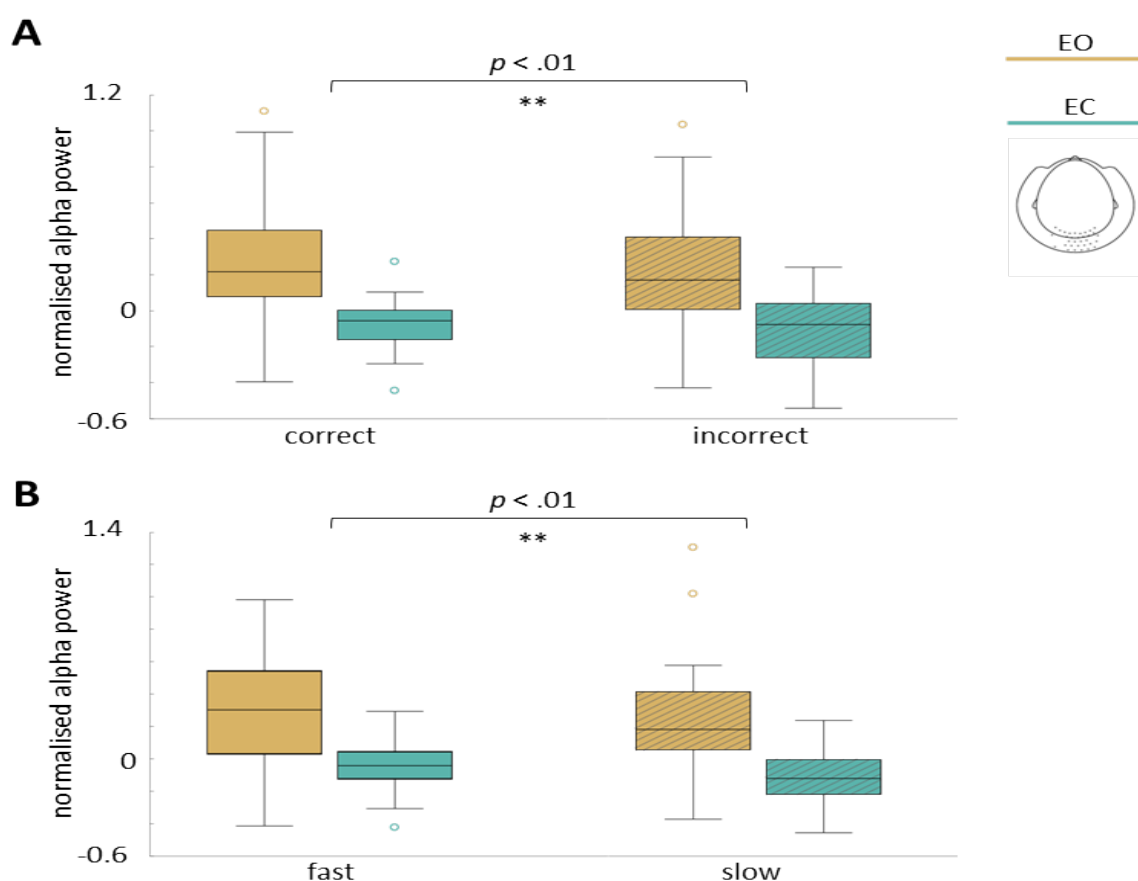
For the RTs, a main effect of performance ( $F(1, 32) = 11.1, p < .01$ ), reflecting increased posterior alpha modulation for faster trials, and eye condition ( $F(1, 32) = 37.34, p < .001$ ), with increased posterior alpha modulation for the EO condition, was found. The interaction of eye condition and performance was not significant ( $F(1, 32) = 0.002, p = .96$ ).

In summary, these results indicate an impact of posterior alpha modulation on behaviour, with better performance following a higher increase of posterior alpha power during the pre-stimulus

interval. This effect was furthermore independent of eye condition.

## Discussion

In this study we aimed to investigate the effect of eye closure on attentional modulations of alpha oscillations and the subsequent behavioural performance during a somatosensory discrimination task. For this we adapted the paradigm by Haegens et al. (2011) to include an eyes-open and an eyes-closed condition. We replicated the lateralization pattern of attentional anticipatory alpha modulation, however found no significant impact on performance outcome. However, we do report a trend of faster reaction times with increased lateralization. Furthermore, though eye closure lead to a general increase of oscillatory activity, it also resulted in a reduced modulation of the posterior alpha power during the pre-stimulus interval in comparison with the eyes-open condition. The posterior alpha



**Figure 6.** Behavioural performance modulation by posterior alpha power. The empty helmet represents the visual ROIs used for this analysis (summary of individual ROIs). P-values represent the main effect of performance. **A.** Modulation by posterior alpha power on discrimination rate (% correct responses). A significant difference of correct and incorrect trials was found, indicating an improved discrimination rate with higher posterior alpha modulation independent of eye condition. **B.** Modulation by posterior alpha power on RTs of correct trials. A significant difference of fast and slow trials was found, indicating a faster performance speed with higher posterior alpha modulation independent of eye condition.

modulation positively influenced task performance, independent of eye condition.

### **Eye closure leads to general increase of reaction times**

Even though we did not formulate prior hypotheses on the effect of eye closure on general performance, we report here an increase of reaction times for the eyes-closed condition in comparison with eyes open, and a tendency of reduced accuracy. This speaks against the anecdotal assumption of improved performance with eye closure, which is thought to lead to better focus towards other sensory modalities (e.g., Glenberg et al., 1998). It furthermore contradicts previous findings of increased somatosensory perception detection associated with eye closure (Brodoehl et al., 2015a). However, these behavioural results are in accordance with a study conducted by Götz et al. (2017), who reported an impairment of somatosensory discrimination with eye closure accompanied by a reduction of somatosensory evoked fields. The authors proposed a possible trade-off between perception that requires spatial discrimination and perception that does not, implicating a negative effect of eye closure on spatial perception. This line of thinking follows from the assumption that eye closure does not only represent a control of visual input, but also influences processing mechanisms of somatosensory information.

### **Eye closure increases alpha power but decreases posterior alpha modulation**

In agreement with previous studies (e.g., Adrian & Matthews, 1934; Geller et al., 2014; Wöstmann et al., 2019), we found an increase of alpha power with eye closure. We furthermore found an additional increase of beta power with eye closure, which was centred towards occipital sensors, while the alpha power increase showed a more widespread pattern. This widespread pattern of increased alpha power with eye closure is in accordance with previous findings (Geller et al., 2014) and indicates that the eye closure effect is not bound to occipital sources. The global increase of alpha further supports the assumption of an eye-closure effect on neural processing, unlike simply reflecting the disengagement of visual areas.

Though eye closure lead to a general increase of alpha power, we furthermore report a reduction of anticipatory posterior alpha modulation in comparison to the eyes-open condition. In this case, modulation of posterior alpha increase

against baseline activity was more prominent, when participants had their eyes open than when their eyes were closed.

Anticipatory alpha power increase has been proposed to reflect a functional mechanism of inhibition to gate information (Jensen & Mazaheri, 2010; Foxe & Snyder, 2011). In the context of somatosensory attention, visual input is not relevant for the completion of the task and therefore increase of alpha activity over occipital regions was proposed to regulate an inhibition of the processing of visual input (Haegens et al., 2012). Our current findings further support this idea, as a much higher increase of posterior alpha synchronization is observed for the condition in which visual input is apparent.

### **Lateralized alpha modulation for both eyes open and eyes closed**

In the context of spatial tactile attention, the inhibitory functional mechanism of alpha oscillations is further reflected by an increase of alpha activity over the ipsilateral and a decrease over the contralateral attentional somatosensory cortex (Haegens et al., 2011; Haegens et al., 2012). We replicated this pattern of contralateral alpha power decrease for both the eyes-open and the eyes-closed condition. Even though we do not observe an ipsilateral increase in our contrasts, this is possibly due to the fact that our study did not include the presentation of distractors. It has been shown, for both the visual (Rihs et al., 2007; Rihs, Michel, & Thut, 2009) as well as the somatosensory domain (Haegens et al., 2012), that ipsilateral increase of alpha is dependent on the presence and the strength of distractors engaging the task-irrelevant side.

The observed lateralization pattern reflected a general decrease of alpha over right somatosensory sensors for left-side attention, and left somatosensory sensors for right-side attention. This further supports the theory that alpha gates the information flow during somatosensory attention tasks, by facilitating excitability in the task relevant somatosensory cortex. However, this interpretation stems purely from the visualisation of spectral sensor activity. Further source analysis is necessary to contrast the activation over somatosensory cortices for a statistical test of significant contralateral alpha activity decrease. Since no source reconstruction was included for this report, no statistical claim and no certainty of the sources of this attentional modulation can be made at this point, as selection of somatosensory ROIs are imprecise on sensor level (see future directions section for more details).

We also investigated the evolution of pre-stimulus alpha modulation over time, which showed a sustained modulation for alpha (around 10 Hz) as well as for beta (around 20 Hz) oscillations for both eye conditions. This indicates that the anticipatory modulation of alpha started after the presentation of the cue and lasted until the presentation of the stimulus, in line with previous studies (e.g., Jensen & Mazaheri, 2010; Haegens et al., 2011; Haegens et al., 2012; Ikkai et al., 2016).

### **No impact of lateralization index on task performance**

The lateralization index reflects the ratio of ipsilateral alpha activity increase and contralateral alpha activity decrease. In previous studies this alpha lateralization index modulated the task performance, leading to better accuracy and faster reaction times with increased lateralization index (Haegens et al., 2011; Haegens et al., 2012). However, we were not able to replicate accuracy effects here, though we did find a trend for RTs, indicating a possible impact of lateralization index on the speed of performance (independent of eye condition). It is worthy to note, that this analysis as well has to be fine-tuned for further interpretational gains (see future directions). Furthermore, for our analysis of RTs we calculated a separation of fast and slow trials based on a median split. This definition of RTs could be improved by binning RTs into multiple ranges from slow to fast (e.g., five instead of two), or by performing a single trial correlation. We plan to address these possibilities in future analysis.

For now, we were not able to replicate an influence on performance through the modulation of alpha lateralization and no influence of eye closure was reported. If these findings translate to later, more precise analyses this would implicate that alpha lateralization is not predictive of task performance.

### **Posterior alpha modulation increases task performance independent of eye condition**

We replicated previous findings of an impact of posterior alpha modulation on task performance both for discrimination rate and RTs (Haegens et al., 2012). In this sense, higher posterior alpha was associated with more accurate and faster responses. This modulation was independent of eye condition. We therefore found evidence that the inhibition of visual processing leads to increased task performance. This is in line with the idea that

through alpha increase over visual regions, resources are gated towards task-relevant brain regions, leading to more successful behavioural outcome. This gating process does not seem to be impacted by eye closure.

In summary, we did observe a steady increase of alpha activity with eye closure, yet the anticipatory alpha modulation showed a higher increase for the eye-open condition. Furthermore, even though posterior alpha modulation showed an impact on the behavioural outcome, this effect was independent of eye condition. This implicates, that the eye closure induced alpha increase and the inhibitory alpha modulation during the EO condition, follow the same mechanism to suppress visual regions and improve the somatosensory task performance.

### **Similar mechanism for alpha and beta?**

Interestingly, we observed similar effects in the beta range (15 – 30 Hz) as for the alpha range. First of all, we observed an eye closure effect not only for alpha but also for beta oscillations. This is not surprising as previous research has indicated an effect of eye closure on all frequency bands to some extent (Geller et al., 2014). We here show — in contrast to previous findings (Geller et al., 2014) — that the beta effect of eye closure was limited to occipital sensors and does not show a widespread pattern like alpha. This could implicate, that with eye closure, unlike alpha, beta does not show a further influence on processing mechanisms outside the occipital cortex, but only reflects an impact of the disengagement of the visual domain.

Regarding anticipatory oscillatory modulation, we observed a sustained contralateral decrease of beta activity for the pre-stimulus interval, similar to the alpha activity. Previous studies proposed that beta follows a similar mechanism as alpha during somatosensory attentional tasks, reflected by a modulation of beta activity in the form of contralateral decrease in anticipation of expected stimuli and an impact of this modulation on performance speed (van Ede, Jensen, & Maris, 2010; van Ede, de Lange, Jensen, & Maris, 2011). However, a study by Haegens et al. (2012) also showed a possible dissociation of alpha and beta in the somatosensory domain, with ipsilateral increased alpha being accompanied by decreased beta activity (see Spitzer & Haegens, 2017, for further discussion on a potential alpha-like role of beta oscillations).

For future investigation of the interplay of these two oscillatory bands, we are planning to expand our analysis to also take into account a possible effect of beta modulation during somatosensory attention.

If the current trend of a similar beta activity to the alpha activity holds true, it would speak for further evidence of similar functions of the two oscillatory bands in the context of somatosensory tasks. Furthermore, it will be interesting to see whether the eye closure effect on beta oscillations, which showed to be specific for occipital sensors, shows a different modulation than for alpha oscillations.

### Future directions

It has to be noted that the results reported here were all conducted on sensor level, which hold the constraint of a mixture of signals from different sources. This complicates possible assumptions of the origins of a signal. Therefore, the selection of our ROIs also followed a less spatially resolved categorisation, with possible contamination of auditory and visual sources. For future directions we plan to move to a source level representation of the data. For this the individual anatomical MRIs of the participants were collected to enable a source reconstruction using beamformer techniques, which allow to counteract the problem of spatial mixing and allow for more precise interpretation of effects.

### Conclusion

We showed a general increase of alpha oscillations with eye closure as long established (Adrian & Matthews, 1934; Geller et al., 2014), with a widespread pattern of alpha, which implicates a possible influence of eye closure on processes outside the visual domain. Furthermore, the findings of this study support the previously proposed mechanism of alpha oscillations to gate information flow in the brain through functional inhibition (Jensen & Mazaheri, 2010; Foxe & Snyder, 2011). In this sense, we showed that alpha power over posterior sensors increased more when available visual input had to be actively inhibited as attention was guided towards the somatosensory domain. This posterior alpha activity increase furthermore has shown to be behaviourally relevant for both eyes conditions, as performance increased with higher alpha activity. This implies that with an increased inhibition of the visual domain, attentional resources are gated towards the somatosensory task, independent of eye condition. We replicated a pattern of contralateral alpha decrease over task-relevant somatosensory sensors, indicating a regulatory role of alpha for facilitation of excitability. However, we did not replicate previous findings of a somatosensory alpha lateralization impact on performance

outcome, which leads to the assumptions that the somatosensory lateralized alpha modulation might only reflect a neural process but does not further influence behaviour. Our behavioural results furthermore contradict an anecdotal assumption of performance improvement with eye closure, as we report an increase of reaction times for the eyes-closed condition. In summary, we provide novel insights into alpha activity during eye closure, showing evidence that while eye closure increased the global alpha activity it did not further impact the inhibitory alpha modulation on performance.

### References

- Adrian E.D., Matthews B.H.C. (1934). The berger rhythm: potential changes from the occipital lobes in man. *Brain*, 57(4), 355–85.
- Banerjee, S., Snyder, A. C., Molholm, S., & Foxe, J. J. (2011). Oscillatory alpha-band mechanisms and the deployment of spatial attention to anticipated auditory and visual target locations: supramodal or sensory-specific control mechanisms? *J Neurosci*, 31(27), 9923-9932.
- Berger, H. (1929). Über das Elektrenkephalogramm des Menschen. *Arch Psychiatr Nervenker*, 87(1), 527-570.
- Bonnefond, M., & Jensen, O. (2012). Alpha Oscillations Serve to Protect Working Memory Maintenance against Anticipated Distracters. *Current Biology*, 22, 1969-1974.
- Brodoehl, S., Klingner, C., Stieglitz, K., & Witte, O. W. (2015a). The impact of eye closure on somatosensory perception in the elderly. *Behav Brain Res*, 293, 89-95.
- Brodoehl, S., Klingner, C. M., & Witte, O. W. (2015b). Eye closure enhances dark night perceptions. *Sci Rep*, 5, 10515.
- Dimitrijevic, A., Smith, M. L., Kadis, D. S., & Moore, D. R. (2017). Cortical Alpha Oscillations Predict Speech Intelligibility. *Front Hum Neurosci*, 11, 88.
- Foxe, J. J., & Snyder, A. C. (2011). The Role of Alpha-Band Brain Oscillations as a Sensory Suppression Mechanism during Selective Attention. *Front Psychol*, 2, 154.
- Geller, A. S., Burke, J. F., Sperling, M. R., Sharan, A. D., Litt, B., Baltuch, G. H., . . . , & Kahana, M. J. (2014). Eye closure causes widespread low-frequency power increase and focal gamma attenuation in the human electrocorticogram. *Clin Neurophysiol*, 125(9), 1764-1773.
- Glenberg, A. M., Schroeder, J. L., & Robertson, D. A. (1998). Averting the gaze disengages the environment and facilitates remembering. *Memory & cognition*, 26(4), 651–658.
- Götz, T., Hanke, D., Huonker, R., Weiss, T., Klingner, C., Brodoehl, S., Baumbach, P., & Witte, O. W. (2017). The Influence of Eye Closure on Somatosensory Discrimination: A Trade-off Between Simple Perception and Discrimination. *Cerebral cortex (New*

- York, N.Y. : 1991), 27(6), 3231–3239.
- Haegens, S., Cousijn, H., Wallis, G., Harrison, P. J., & Nobre, A. C. (2014). Inter- and intra-individual variability in alpha peak frequency. *NeuroImage*, 92(100), 46–55.
- Haegens, S., Händel, B. F., & Jensen, O. (2011). Top-down controlled alpha band activity in somatosensory areas determines behavioral performance in a discrimination task. *Journal of Neuroscience*, 31, 5197–5204.
- Haegens, S., Luther, L., & Jensen, O. (2012). Somatosensory Anticipatory Alpha Activity Increases to Suppress Distracting Input. *Journal of Cognitive Neuroscience*, 24, 677–685.
- Haegens, S., Nächer, V., Luna, R., Romo, R., & Jensen, O. (2011).  $\alpha$ -Oscillations in the monkey sensorimotor network influence discrimination performance by rhythmical inhibition of neuronal spiking. *Proceedings of the National Academy of Sciences of the United States of America*, 108(48), 19377–19382.
- Haegens, S., Osipova, D., Oostenveld, R., & Jensen, O. (2010). Somatosensory working memory performance in humans depends on both engagement and disengagement of regions in a distributed network. *Human Brain Mapping*, 31, 26–35.
- Ikkai, A., Dandekar, S., & Curtis, C.E. (2016). Lateralization in Alpha-Band Oscillations Predicts the Locus and Spatial Distribution of Attention. *PLoS ONE*, 11.
- Jensen, O., & Mazaheri, A. (2010). Shaping functional architecture by oscillatory alpha activity: gating by inhibition. *Front Hum Neurosci*, 4, 186.
- Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG- and MEG-data. *Journal of Neuroscience Methods*, 164, 177–190.
- Kelly, S. P., Gomez-Ramirez, M., & Foxe, J. J. (2009). The strength of anticipatory spatial biasing predicts target discrimination at attended locations: a high-density EEG study. *The European journal of neuroscience*, 30(11), 2224–2234.
- Klimesch, W., Sauseng, P., & Hanslmayr, S. (2007). EEG alpha oscillations: the inhibition-timing hypothesis. *Brain research reviews*, 53(1), 63–88.
- Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J.-M. (2011). FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Computational Intelligence and Neuroscience*, 2011(156869), 1–9.
- Pfurtscheller, G., & Klimesch, W. (1991). Event-related desynchronization during motor behavior and visual information processing. *Electroencephalography and clinical neurophysiology. Supplement*, 42, 58–65.
- Rihs, T. A., Michel, C. M., & Thut, G. (2007). Mechanisms of selective inhibition in visual spatial attention are indexed by  $\alpha$ -band EEG synchronization. *European Journal of Neuroscience*, 25, 603–610.
- Rihs, T. A., Michel, C. M., & Thut, G. (2009). A bias for posterior alpha-band power suppression versus enhancement during shifting versus maintenance of spatial attention. *Neuroimage*, 44, 190–199.
- Sauseng, P., Klimesch, W., Stadler, W., Schabus, M., Doppelmayr, M., Hanslmayr, S., et al. (2005). A shift of visual spatial attention is selectively associated with human EEG alpha activity. *European Journal of Neuroscience*, 22, 2917–2926.
- Spitzer, B., & Haegens, S. (2017). Beyond the Status Quo: A Role for Beta Oscillations in Endogenous Content (Re)Activation. *eNeuro*, 4(4), ENEURO.0170-17.2017.
- Strauß, A., Wöstmann, M., & Obleser, J. (2014). Cortical alpha oscillations as a tool for auditory selective inhibition. *Front Hum Neurosci*, 8:350.
- Thut, G., Nietzel, A., Brandt, S. A., & Pascual-Leone, A. (2006). Alpha-band electroencephalographic activity over occipital cortex indexes visuospatial attention bias and predicts visual target detection. *Journal of Neuroscience*, 26, 9494–9502.
- van Albada, S. J., & Robinson, P. A. (2013). Relationships between Electroencephalographic Spectral Peaks Across Frequency Bands. *Frontiers in human neuroscience*, 7, 56.
- van Ede, F., de Lange, F., Jensen, O., & Maris, E. (2011). Orienting attention to an upcoming tactile event involves a spatially and temporally specific modulation of sensorimotor alpha- and beta-band oscillations. *Journal of Neuroscience*, 31, 2016–2024.
- van Ede, F., Jensen, O., & Maris, E. (2010). Tactile expectation modulates prestimulus beta-band oscillations in human sensorimotor cortex. *Neuroimage*, 51, 867–876.
- Vredeveltdt, A., Baddeley, A. D., & Hitch, G. J. (2012). The Effects of Eye-Closure and “Ear-Closure” on Recall of Visual and Auditory Aspects of a Criminal Event. *Europe’s Journal of Psychology*, 8(2), 284-299.
- Vredeveltdt, A., Tredoux, C. G., Nortje, A., Kempen, K., Puljevic, C., & Labuschagne, G. N. (2015). A field evaluation of the Eye-Closure Interview with witnesses of serious crimes. *Law Hum Behav*, 39(2), 189-197.
- Worden, M. S., Foxe, J. J., Wang, N., & Simpson, G. V. (2000). Anticipatory biasing of visuospatial attention indexed by retinotopically specific alpha-band electroencephalography increases over occipital cortex. *Journal of Neuroscience*, 20, RC63.
- Wöstmann, M., Schmitt, L., & Obleser, J. (2019). Does Closing the Eyes Enhance Auditory Attention? Eye Closure Increases Attentional Alpha-Power Modulation but Not Listening Performance. *Journal of Cognitive Neuroscience*, 32, 212-225.

## Supplementary Material

### Methods of visualisation

To visualize attention effects within the pre-stimulus interval, we evaluated the pre-stimulus FFT based on whether attention was being guided to the left or the right hand (dependent on the auditory cue). For this, we divided trials into four conditions: EO attention-right, EO attention-left, EC attention-right, and EC attention-left. A baseline correction was applied based on the FFT of the baseline window -1 s to 0 s of cue-onset. Baseline corrections were done separately for EO and EC trials. For each attention side of each condition the whole-head power distributions were computed.

For a visualisation of the lateralization pattern the pre-stimulus FFT was once again divided into the four conditions, based on eye-condition and attention-side, but not baseline corrected. Instead, a normalization in the form of  $(\text{attention-left} - \text{attention-right}) / (\text{attention-left} + \text{attention-right})$  was computed for each eye-condition separately. This normalization leads to positive values if there is a stronger decrease in the attention-right condition and negative values for a stronger decrease in the attention-left condition.

To obtain a representation of the modulation of alpha activity over time, the TFR of the pre-stimulus interval (-1 s – 0 s) was divided into EO and EC trials and baseline corrected (with baseline -1.5 s – -1 s) for each condition separately. As before, the left vs right normalization of attention sides was applied for the two conditions. Only the individual somatosensory ROIs were used for this visualisation. Left hemispheric sensors were mirrored to combine them with the right hemispheric sensors, leading to a general representation of the decrease of activity. Power spectra of low frequencies in the range of 5 to 30 Hz were used for this visualisation.