

Relating alpha power modulations to competing visuospatial attention theories

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ABSTRACT

Visuospatial attention theories often propose hemispheric asymmetries underlying the control of attention. In general support of these theories, previous EEG/MEG studies have shown that spatial attention is associated with hemispheric modulation of posterior alpha power (gating by inhibition). However, since measures of alpha power are typically expressed as lateralization scores, or collapsed across left and right attention shifts, the individual hemispheric contribution to the attentional control mechanism remains unclear. This is, however, the most crucial and decisive aspect in which the currently competing attention theories continue to disagree. To resolve this long-standing conflict, we derived predictions regarding alpha power modulations from Heilman's hemispacial theory and Kinsbourne's interhemispheric competition theory and tested them empirically in an EEG experiment. We used an attention paradigm capable of isolating alpha power modulation in two attentional states, namely attentional bias in a neutral cue condition and spatial orienting following directional cues. Differential alpha modulations were found for both hemispheres across conditions. When anticipating peripheral visual targets without preceding directional cues (neutral condition), posterior alpha power in the left hemisphere was generally lower and more strongly modulated than in the right hemisphere, in line with the interhemispheric competition theory. Intriguingly, however, while alpha power in the right hemisphere was modulated by both, cue-directed leftward and rightward attention shifts, the left hemisphere only showed modulations by rightward shifts of spatial attention, in line with the hemispacial theory. This suggests that the two theories may not be mutually exclusive, but rather apply to different attentional states.

1. Introduction

Visuospatial attention allows selection and suppression of incoming visual information. Current functional-anatomical models agree on the importance of fronto-parietal networks in attentional control and emphasize hemispheric asymmetries in their functional organization. However, there is long-standing disagreement regarding the exact role of each hemisphere in attention and their interactions. This becomes particularly apparent in the divergent attempts to explain why attention deficits following unilateral brain damage (hemineglect) are commonly more severe and prevalent after right hemispheric damage (Corbetta et al., 2005).

The '*hemispacial*' theory states that the right hemisphere is involved when attending to the left and right hemifields, whereas the left

hemisphere is only involved when attending to the right hemifield (Heilman & Van Den Abell, 1980). Hemineglect would thus originate from a loss of function, with right hemisphere damage causing attention deficits in the left hemifield because the intact left hemisphere is restricted to the right hemifield, whereas left hemisphere damage can be compensated for because the intact right hemisphere encompasses both hemifields. In some sense, this functional asymmetry can be considered a right hemispheric dominance in attention.

In contrast, the '*interhemispheric competition*' theory proposes that competitive interactions between hemispheres lead to prioritization of one hemifield over the other (Kinsbourne, 1977). Each hemisphere exerts a bias toward the contralateral hemifield and they mutually inhibit each other via transcallosal connections. An often overlooked aspect of this theory is that the rightward bias of the left hemisphere is argued to be

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stronger than the leftward bias of the right hemisphere. Consequently, hemineglect should not be described as a loss of function but it rather reflects severely biased competition between hemispheres. Right hemisphere damage leaves the stronger rightward bias of the left hemisphere unopposed forcing attention away from the left hemifield, whereas left hemisphere damage only exposes the relatively mild leftward bias of the right hemisphere. This hemispheric asymmetry can be considered a left hemispheric dominance in attention.

A separate line of research has focused on the role of posterior oscillatory brain activity within the alpha range (7–13 Hz) either using tasks explicitly requiring voluntary shifts of spatial attention (Dombrowe and Hilgetag, 2014; Rihs et al., 2007; Sauseng et al., 2005; Worden et al., 2000; Yamagishi et al., 2005) or implicitly assessing attentional processes by probing variations in perceptual performance (Hanslmayr et al., 2007; Lange et al., 2013; van Dijk et al., 2008). Voluntary shifts of attention to one hemifield have generally been found to be associated with alpha power lateralization, typically resulting from contralateral decreases and/or ipsilateral increases of alpha power relative to the locus of spatial attention (Gould et al., 2011; Händel et al., 2011; Kelly et al., 2006; Rihs et al., 2007; Rihs et al., 2009; Sauseng et al., 2005; Thut et al., 2006; Worden et al., 2000; Yamagishi et al., 2003, 2005). Similarly, alpha power prior to the presentation of visual stimuli is predictive of general task performance (Händel et al., 2011; Hanslmayr et al., 2007; Thut et al., 2006; van Dijk et al., 2008), but has also been linked to spatially-specific attentional biases that spontaneously occur in visual tasks (Boncompagni et al., 2016).

Alpha power can thus serve as an index of attentional control processes. Importantly, alpha oscillations are widely thought to reflect inhibitory processes, and alpha power lateralization may thus be interpreted as a mechanism that facilitates stimulus processing by i) enhancing responses at attended locations (Hopfinger et al., 2000; Kastner et al., 1999) and ii) suppressing potential distractors at unattended locations (Jensen and Mazaheri, 2010; Klimesch et al., 2007).

Based on the two aforementioned models of attentional control, diverging predictions regarding alpha power modulation can be derived: according to the hemispatial theory, attention allocation to the left visual field involves only the right hemisphere; so only a right hemispheric alpha power decrease is expected. In attention allocation to the right visual field both hemispheres are involved, suggesting bilateral alpha power modulation with a left hemispheric decrease and a right hemispheric increase. According to the interhemispheric competition theory, the balance between hemispheres determines the locus of attention, with the left hemisphere generating a stronger rightward bias as compared to the leftward bias generated by the right hemisphere. This left hemispheric dominance could be observable in different levels of alpha power between left and right hemispheres. Additionally, competitive interactions between hemispheres are predicted to occur during shifts of attention, implying that attention allocation toward either hemifield leads to bilateral alpha power modulation with a contralateral alpha power decrease and an ipsilateral alpha power increase. The recurring observation in the literature of alpha power lateralization in some sense matches key aspects of this interhemispheric competition theory, but this correspondence might be misleading, as it will be shown below.

The vast majority of previous studies has focused on alpha power lateralization indices, thus quantifying the difference in alpha power between the left and right hemispheres (Händel et al., 2011; Kelly et al., 2006; Rihs et al., 2009; Sauseng et al., 2005; Thut et al., 2006; Worden et al., 2000), or directly contrasted leftward and rightward attentional shifts, thereby ignoring hemifield-specific contributions by collapsing the assumed contralateral decreases and ipsilateral increases (Marshall, O'Shea, Jensen and Bergmann, 2015). The observed lateralization might arise from contralateral decreases, ipsilateral increases or both (Kelly et al., 2006; Rihs et al., 2009; Sauseng et al., 2005; Worden et al., 2000). Therefore, this collapsing of data across hemifields and/or hemispheres fails to reveal potentially important hemispheric asymmetries. Moreover, it is common practice to reference alpha power during attention shifts to

alpha power prior to attention shifts (Ikka et al., 2016; Kelly et al., 2006; van Diepen et al., 2016; Wildegger et al., 2017). However, this procedure may fail to control for other task-related preparatory activities. The inclusion of a baseline condition (neutral cues) that accounts for such effects may allow isolating alpha power changes specific to attention shifts without such confounders.

We set out to relate alpha power modulations to Kinsbourne's inter-hemispheric competition theory and Heilman's hemispatial theory. Surprisingly, despite the well-established relation between alpha power and attention, such a full characterization of alpha power modulations across hemispheres and attentional states (bias at "baseline" versus shifts of attention) is still lacking. We here report alpha power changes during a spatial orienting paradigm for each hemisphere and three attention conditions separately. We first explored the dynamics of posterior alpha power in a neutral cue condition that does not require any shifts of attention (baseline), thus relating to the concept of attentional bias. We then assessed the magnitude of alpha power up- and down-regulation for leftward and rightward attention shifts relative to that baseline. Critically, this allowed us to control for task effects that are shared by directional and non-directional cues, normally not identifiable when comparing to a pre-cue baseline. By using this approach, we were able to directly test the key predictions derived from competing models of attentional control in two attentional states.

2. Material and methods

2.1. Overall study design

The results presented here are part of a larger project involving functional magnetic resonance imaging (fMRI), transcranial magnetic stimulation (TMS) and electroencephalography (EEG). The project included one fMRI session for frontal eye fields (FEFs) localization and three TMS sessions counterbalanced in a within-subjects design. TMS studies commonly involve a placebo condition: the data reported here stem from EEG sessions that were preceded by 40 s of offline placebo TMS with no direct neural effects.

2.2. Participants

Twenty-seven healthy participants took part in the experiment (8 men, M age: 21.9, SD: 2.5). All of them were right-handed, had normal or corrected-to-normal vision and did not report any history of neurological or psychiatric disorders. Before each session participants provided written informed consent and filled out a screening form for TMS contraindications. The study was approved by the Ethics Review Committee Psychology and Neuroscience at Maastricht University.

2.3. Procedure

Before starting the task, participants performed a short practice session identical to the real task, except that they received feedback on their performance. In this practice session we ensured that performance was sufficiently accurate and fast, and modulated by presented symbolic cues (see below). Next, an EEG cap was prepared using electroconductive paste (MedCat, OneStep ClearGel, Klazienaveen, The Netherlands). Participants received fMRI-guided placebo TMS over either the left or the right FEF using a continuous theta burst stimulation protocol (50-Hz triplets were delivered 5 times a second for 40 s, 600 pulses in total). TMS was delivered with a purpose-built placebo TMS coil (MC-P-B70, MagVenture, Farum, Denmark) with strong attenuation of the magnetic field so that no effective stimulation occurred. The stimulation site was counterbalanced across participants, targeting the left FEF in half of the cases and the right FEF in the other half. After the stimulation, participants were seated in front of a computer screen with their head supported by a chin rest at a viewing distance of 57 cm. As already indicated above, data were recorded without neuromodulation, and without any placebo

TMS during task execution. There was only a 40-s placebo TMS protocol at the start of the experimental session, after which all TMS equipment was removed.

2.4. Task and stimuli

During the EEG measurements, participants performed a spatial orienting task consisting of 504 trials divided in 6 blocks composed of 84 trials each (plus 4 warm-up trials included at the beginning of each block). The task took around 40 min to complete. Visual stimuli were presented on a gamma corrected 24-inch monitor (Iiyama ProLite B2481HS-B1, Iiyama, Japan) using a 1920 × 1080 (60 Hz) mode. The software Presentation (version 19.0, NeuroBehavioral System, Albany, CA) was used to display visual stimuli and record behavioral responses.

Symbolic cues were used to direct covert shifts of visual attention in space (Posner, 1980). During the task, a black dot was constantly shown at the center of the screen (•). The start of a trial was announced by a circle presented around the central dot (⊙) 100 ms before cue onset. Spatial cues consisted of two double arrowheads next to the central dot pointing leftward (◀◀•◀◀) or rightward (▶▶•▶▶), prompting participants' covert attention toward one hemifield. The neutral cue consisted of two double arrowheads pointing in opposite directions (◀◀•▶▶), providing temporal but not spatial information. The cue duration was 100 ms, after which there was an interval of 1500 ms before the appearance of the target (i.e. stimulus onset asynchrony [SOA] 1600 ms). Target stimuli were Gabor patches (spatial frequency = 1.5 cycles per degree, envelope standard deviations = 0.75°, Michelson contrast = 60%, randomly tilted 45° to the left or right) presented for 100 ms at 7° eccentricity either on the left or right side of the fixation point. Participants were instructed to identify the target orientation independently of its location, and respond as quickly and accurately as possible. They responded using a computer keyboard, pressing Numpad1 (left orientation) using the right index finger or Numpad2 (right orientation) using the right middle finger. The button press ended the trial; onset of the next trial followed after either 800, 1000, or 1200 ms.

Trials were defined as *valid* when cue direction and target position were congruent (e.g. cue pointing to the right, target appearing on the

right side of the fixation point), *neutral* in the case of a neutral cue, and *invalid* when cue direction and target position were incongruent (e.g. cue pointing to the right, target appearing on the left side of the fixation point). Fig. 1 shows an example of a trial. The combination of the three types of cue (left, right, and neutral) and the two positions of the target (left, right) resulted in six conditions. The presentation frequency of valid, neutral and invalid trials was not equally balanced across conditions but had a ratio of 4:2:1 respectively, to ensure that symbolic cues were sufficiently informative.

2.5. EEG recording and pre-processing

2.5.1. Recording

Brain activity was recorded using a 64-channel EEG system (EasyCap, Brain Products GmbH, Munich, Germany) composed of sintered Ag/AgCl TMS-compatible passive electrodes placed over the scalp according to the 10/10 international system. Electro-oculography (EOG) was used to record eye artifacts. EOG electrodes measuring horizontal eye movements were positioned on the outer canthi of the left and right eyes, whereas vertical eye movements were identified from two electrodes, one placed below the left eye and Fp1. FCz was used as a reference electrode and AFz as a ground electrode. During the recording the signal was amplified by using 2 amplifiers of 32 channels each (Brain Products GmbH, Munich, Germany), digitized using a sampling rate of 500 Hz, and stored on a hard disk using the software BrainVision Recorder (BrainProducts GmbH, Munich, Germany). The impedance of the signal was kept below 5 KΩ and online low-pass (100 Hz), high-pass (0.53 Hz) and notch (50 Hz) filters were used.

2.5.2. Pre-processing

EEG data were preprocessed and analyzed using both custom-written Matlab scripts (The MathWorks Inc., Natick, USA, version 2014a) and the FieldTrip toolbox version 2014 (Oostenveld et al., 2011). The signal was epoched in segments of 2.9 s starting at 0.8 s before and ending at 2.1 s after the onset of the cue (time 0). After this process a low-pass filter at 60 Hz was applied. The filtered EEG activity was offline re-referenced to the mean activity of all EEG channels. For the identification of “eye

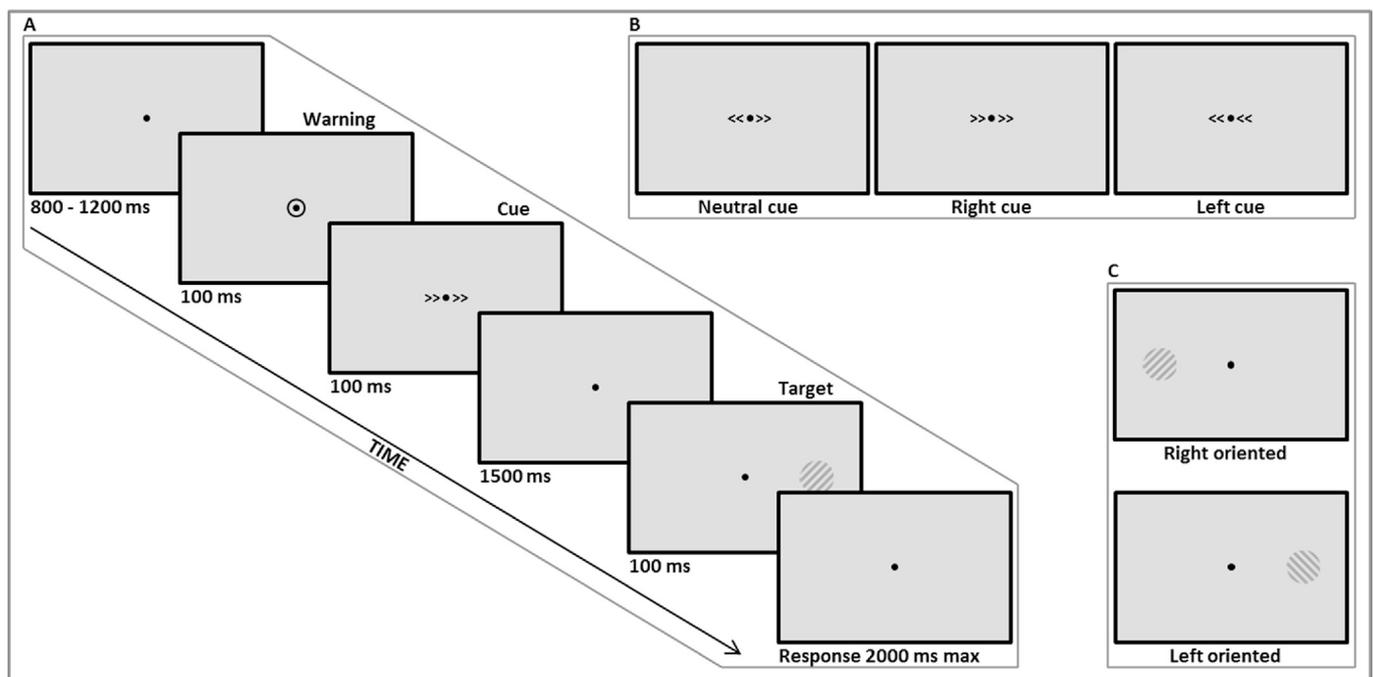


Fig. 1. A) Representation of a possible trial and the time intervals between trial events; in this example (a valid trial) the cue prompts attention toward the right hemifield and the target appears at the same location. B) Neutral and spatial (left and right) cues. C) Possible target locations (left, right) and orientations (right oriented, left oriented).

movement-contaminated" trials we used two approaches: taking advantage of the eye channels we firstly performed a visual inspection of each trial and removed the ones containing blinks and/or saccades. This step was done to assure that within the time window of our interest (cue-target interval [0–1.6 s]) no eye movements occurred. Secondly, an independent component analysis (ICA) was used to identify other types of artifact (e.g. muscle movements, amplifier saturation) and to detect the remaining eye movement artifacts occurred outside of the time period included in the previous inspection [-0.8 - 0 s, 1.6–2.1 s] (Jung et al., 2000). The proportion of trials not included in the subsequent analyses was 17.1% on average. This proportion was similar across conditions.

2.6. EEG analysis

A time-frequency analysis was performed using the Morlet wavelet approach. The sliding wavelet had a constant length of 300 ms, whereas its number of cycles varied in a frequency-dependent manner and was obtained by multiplying the frequency of interest by the length of the wavelet in seconds (i.e. n° cycles = frequency \times 0.3 s). The wavelet moved along frequencies in steps of 0.5 Hz from 5 Hz to 30 Hz and along time points in steps of 50 ms throughout the entire epoch [-0.8–2.1 s]. Given that our analyses described below exclusively focused on a narrow frequency band (alpha), this approach may seem unnecessarily convoluted. The primary motivation for this was to ensure comparability of the present study with planned analyses of our TMS conditions (not reported here) which will ultimately be compared to a TMS/MEG study by Marshall et al. (2015) who used a similar approach.

2.7. Statistical analysis of behavioral data

Individual mean reaction times (RTs) were based on trials with correct responses, and analyzed in a 3×2 repeated-measures analysis of variance (ANOVA) with Cue Validity (valid, neutral and invalid) and Hemifield (left and right) as within-subject factors. Greenhouse-Geisser correction was applied to compensate the violation of assumed sphericity for the factor Cue Validity. Follow-up *t*-tests were then performed to investigate RT differences between valid trials and neutral trials, and between invalid trials and neutral trials.

2.8. Statistical analysis of EEG data

Data of one participant were not included in the analyses due to technical problems during data acquisition, and data of two participants were excluded from the analyses due to statistical outliers in the within-subject differences (>1.5 times the interquartile range away from the 25th or the 75th percentile of the samples) either in the neutral or in the spatial cue conditions. EEG analysis was performed on data from the remaining 24 participants. Since we were interested in the modulation of posterior alpha-band activity in a specific time interval, the statistical analysis was performed on subsets of channels, frequencies and time points. The alpha power estimation was obtained for right parietal cortex (PO4, PO8, P4, P6, P8) and left parietal cortex (PO3, PO7, P3, P5, P7) separately, by averaging the time-frequency analysis results over channels and alpha-frequency bins (7–13 Hz).

We performed three sets of analyses that are outlined below. For neutral cue trials, we were interested in general alpha power differences between hemispheres in the absence of attention shifts, but also in the dynamics of alpha power changes during the cue-target interval to illustrate the need for this control condition when isolating orienting-specific processes. For directional cue trials, we focused on the critical period of the cue-target interval when alpha power modulation related to shifts of attention is expected to occur. Lastly, we performed two conventional analyses that do not take advantage of a neutral cue condition, mainly for the purpose of comparison but also to emphasize the added value of our methodology.

2.8.1. Neutral cue

We first evaluated whether there was an overall difference in hemispheric engagement, over the whole epoch, as indexed by an absolute alpha power difference between hemispheres. Since this analysis involves comparisons of raw alpha power, as opposed to baseline-corrected alpha power as below, we performed a logarithmic transformation of alpha power at the single-epoch level (Smulders, ten Oever, Donkers, Quaedflieg and van de Ven, 2018), which has previously been shown to sufficiently counter variability of raw alpha power over trials within participants (Haegens et al., 2014; Smulders et al., 2018) and between participants (Haegens et al., 2014; Klimesch, 1999). Though primarily interested in an overall alpha power difference between hemispheres (collapsed over the epoch [-0.65–1.45 s], compared in a paired samples *t*-test), we also checked whether this difference changed within the epoch. For this, we compared alpha power for each time point of the epoch using Monte Carlo simulations to estimate *p*-values with 10,000 randomizations. Multiple comparison correction was implemented at cluster level with an alpha of 0.05, and by controlling the family-wise error rate using the cluster statistics also at an alpha of 0.05 (Maris, 2012).

Secondly, we assessed for each hemisphere how it responded to alerting cues. To test this, we measured whether neutral cues modulated alpha power. We now baseline-corrected (relative change, baseline period: [-0.65 to -0.25 s]) the (not log-transformed) raw alpha power averaged over trials. Baseline-corrected values were then tested against 0, separately per time point and cluster-threshold corrected for multiple corrections as above. We then collapsed the data over time [0.4–1.45 s] and tested left and right hemispheres against each other using a paired samples *t*-test.

2.8.2. Spatial cues

To test whether the magnitude of alpha power was significantly different between neutral and spatial cues we normalized (i.e. divided) every time-point of raw alpha power (not log-transformed) in response to spatial cues by the corresponding time-point of raw alpha power obtained from the neutral cue (no attentional shifts). We then averaged time points within the cue-target interval, when we expected alpha power modulation related to the shift of attention. To prevent confounding of the alpha power estimate with the event-related activity generated by the presentation of the cue, the epoch of interest started after the visual processing of the cue and ended 150 ms before the target onset [0.4–1.45 s]. The results were tested against 1 using a one-tailed paired samples *t*-test, based on clear a priori hypotheses about the expected directionality of alpha power modulation in these analyses. This computation allowed us to reveal alpha power changes related to left and right attentional shifts compared to no attentional shifts, separately per hemisphere. Lastly, we computed a 2×2 ANOVA with Hemifield (contralateral, ipsilateral) and Hemisphere (left, right) as within-subject factors and, to formally quantify the absolute magnitude difference between these conditions, two paired samples *t*-tests for both hemispheres.

2.8.3. Baseline correction and attentional modulation index approaches

To better understand the benefits of normalizing the data by the neutral cue, we also performed two conventional analysis approaches of the directional cue conditions. First, we used standard baseline correction of the raw alpha power (absolute, baseline period: [-0.65 to -0.25 s]) to check how alpha power changed during the cue-target interval as compared to the pre-cue period. The levels of alpha power for left and right hemispheres were then tested against 0 using paired samples *t*-tests. Second, we computed an attentional modulation index (AMI) by subtracting the raw alpha power related to right shifts of attention from the alpha power related to left shifts of attention and then dividing by their average. In principle, the AMI should reveal the traditional pattern of ipsilateral alpha power increase and contralateral decrease and we therefore tested alpha power for the left and right hemispheres against 0 using paired samples *t*-tests.

3. Results

3.1. Behavioral

We first evaluated whether attentional cues (valid, invalid, neutral) modulated reaction times to targets presented to either Hemifield (left, right). The repeated-measures ANOVA showed significant main effects of Cue ($F_{(1,185,27.260)} = 45.627, p < .001$) and Hemifield ($F_{(1,23)} = 7.110, p < .05$), and a non-significant Cue \times Hemifield interaction ($F_{(2,46)} = 3.096, p > .05$). The main effect of Cue was further investigated with follow-up t-tests showing faster RTs for valid trials ($t_{(23)} = -6.398, p < .001$) and slower RTs for invalid trials ($t_{(23)} = 5.963, p < .001$) both compared to neutral trials (see Fig. 2). The presence of attentional benefits and attentional costs in our reaction time data demonstrates that participants covertly shifted their attention toward the cued locations. This was expected based on our previous results (Duecker et al., 2013), but not trivial given the much longer cue-target SOA (1600 ms) we used compared to our previous implementations (600 ms). The replication of these behavioral results with the current parameters was a crucial prerequisite for the EEG analysis, allowing us to investigate alpha power modulations in the longer cue-target interval in response to attentional shifts. The main effect of Hemifield resulted from faster RTs for targets presented in the right hemifield, probably because participants responded with the right hand, leading to the Simon effect (Simon and Rudell, 1967).

3.2. EEG

3.2.1. Neutral cue

Logarithmically transformed alpha power in the left hemisphere was overall (collapsed over the entire epoch) lower than in the right hemisphere ($t_{(23)} = 2.886, p < .01$; Fig. 3A, top right panel). Over the course of the epoch, we found three clusters with statistically significant differences (cluster statistics, early to late: 14.055, $p < .03$, 12.430, $p < .05$, 68.317, $p < .01$; Fig. 3A).

To understand how much the presentation of a neutral cue (no attentional shifts) influenced alpha power in each hemisphere, baseline-corrected alpha power was tested against 0 for the left and the right hemispheres separately. In both hemispheres alpha power decreased after the presentation of the cue (cluster statistics, early to late for the left hemisphere: $-12.8468, p < .05$, $-166.664, p < .0001$ and for the right hemisphere: $-22.8451, p < .03$, $-82.8825, p < .0001$, $-22.1266, p < .03$; Fig. 3B). After the presentation of the neutral cue the left hemisphere showed a greater negative alpha power modulation compared to the

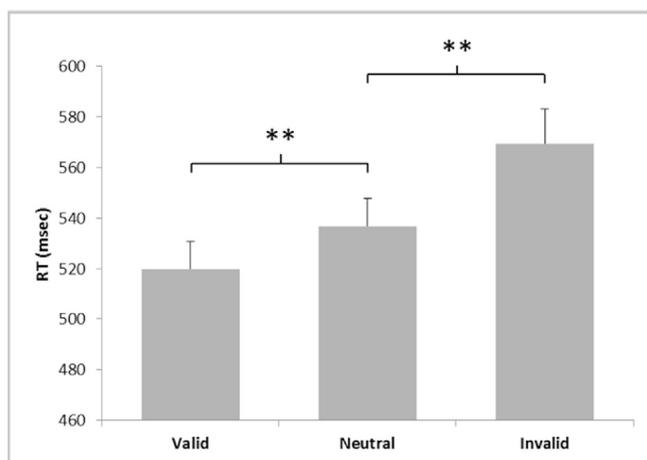


Fig. 2. Reaction times (RTs) for valid, neutral and invalid trials. Differences between bars marked with two asterisks are statistically significant ($p < .001$); error bars represent SEM across subjects.

right hemisphere (cluster statistics, over time: $-10.1301, p < .05$; averaged over time [0.4–1.45 s]: $t_{(23)} = -2.441, p < .03$, Fig. 3B). This might suggest that the left hemisphere more successfully maintains a state of alertness after an alerting cue, thus creating an attentional bias at baseline.

3.2.2. Spatial cues

To reveal the magnitude and direction of spatial cue-induced alpha power changes separately for the left and right hemispheres, we normalized (i.e. divided) the spatial cues alpha power levels to the alpha power level obtained in the neutral cue condition. This means the results isolate the spatial orienting component in the alpha modulation, having controlled for the temporal and alerting effects of cues. Topoplots and bars shown in Fig. 4 B depict normalized alpha power averaged across time points from 0.4 s to 1.45 s after the presentation of the cue.

In the right hemisphere alpha power increased ($t_{(23)} = 2.005, p < .03$) when attention was deployed to the ipsilateral side (right cue condition), whereas it decreased ($t_{(23)} = -3.236, p < .01$) when attention was deployed to the contralateral side (left cue condition) in both cases compared to when attention was not deployed in visual space (neutral cue condition). In the left hemisphere alpha power was modulated differently. While it decreased when attention was deployed to the contralateral side ($t_{(23)} = -2.286, p < .03$), it did not increase when attention was deployed to the ipsilateral side ($t_{(23)} = -0.047, p > .51$).

Complementary to the planned t-tests, we performed a 2×2 ANOVA to evaluate whether there was any difference in the magnitude of the obtained alpha power modulations. In line with the t-tests, the analysis showed a Hemisphere \times Hemifield interaction approaching significance ($F_{(1,23)} = 3.978, p < .06$), a main effect of Hemifield ($F_{(1,23)} = 77.0654, p < .001$) and no effect of Hemisphere ($F_{(1,23)} = 1.649, p > .21$). In light of the results obtained from the previous analysis we performed a further investigation of the interaction. Follow-up t-tests showed a significant difference when attention was shifted to the ipsilateral side of space between left and right hemispheres ($t_{(23)} = -2.099, p < .05$) and no difference when attention was shifted to the contralateral side of space ($t_{(23)} = 0.731, p > .47$).

3.2.3. Baseline correction and attentional modulation index

To illustrate the benefit of normalizing to a neutral cue condition, we also analyzed the same data using two conventional approaches. Fig. 5A depicts the alpha power level averaged across time points from 0.4 to 1.45 s after the presentation of the cue, obtained for the left and right attention conditions after having applied baseline correction. The topoplots and the bar graphs show that alpha power generally decreased after the presentation of the cue in both hemispheres for the left attention condition (left hemisphere: $t_{(23)} = -4.537, p < .001$, right hemisphere: $t_{(23)} = -5.038, p < .001$) as well as for the right attention condition (left hemisphere: $t_{(23)} = -5.491, p < .001$, right hemisphere: $t_{(23)} = -2.293, p < .05$). Importantly, no significant differences were found between hemispheres (left vs right hemisphere for the left attention condition: $t_{(23)} = 1.218, p > .23$, left vs right hemisphere for the right attention condition: $t_{(23)} = -1.613, p > .12$).

Fig. 5B shows alpha power levels expressed as attentional modulation index, averaged across time points from 0.4 to 1.45 s after the presentation of the cue. As the topoplot shows, this resulted in the well-known pattern of alpha power increase in the left hemisphere and decrease in the right hemisphere compared to 0 (left hemisphere: $t_{(23)} = 2.355, p < .03$, right hemisphere: $t_{(23)} = -5.995, p < .001$). This method is able to reveal alpha power lateralization in response to directional cues, but since data are collapsed across hemifields it does not reveal the single hemispheric contribution to these attentional processes.

4. Discussion

Several theories have postulated a hemispheric asymmetry for the control of visuospatial attention (Corbetta and Shulman, 2011; Duecker

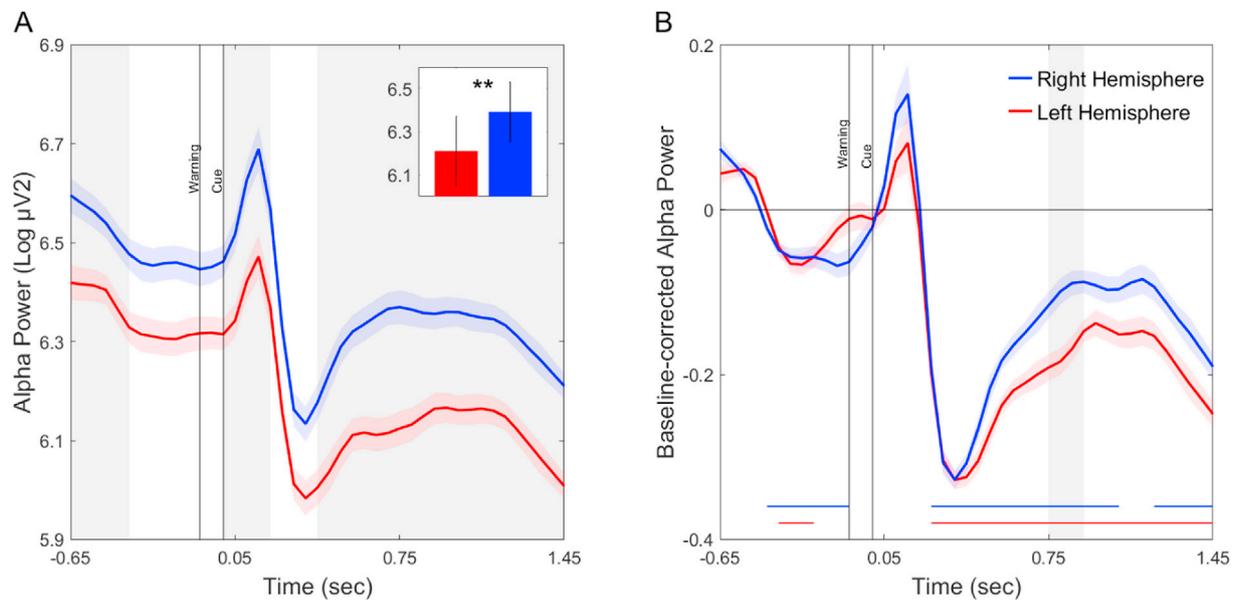


Fig. 3. **A)** Time evolution of log-transformed alpha power for the left (red line) and right (blue line) hemispheres. Light red and light blue areas represent SEM across subjects. Light grey areas represent the time windows in which the two time courses significantly differ from each other ($p < .05$, cluster correction). The two bars in the top right panel represent alpha power levels averaged over time throughout the entire epoch [-0.65 - 1.45]; the two asterisks represent a significant difference between bars ($p < .01$); error bars represent SEM across subjects. **B)** Time evolution of baseline-corrected (baseline period: [-0.65 to -0.25]) alpha power for the left (red line) and right (blue line) hemispheres. Lines in the baseline period are above and below 0, leading to an average value of 0. Light red and light blue areas represent SEM across subjects. The light grey area represents the time window in which the two time courses significantly differ from each other ($p < .05$, cluster correction). Red and blue lines at the bottom of the figure represent the time windows in which the two time courses significantly differ from 0 ($p < .05$, cluster correction).

and Sack, 2015; Heilman & Van Den Abell, 1980; Kinsbourne, 1977), but which theory successfully predicts the hemispheric dynamics related to the allocation of attention is still a matter of debate. The aim of this study was to test predictions derived from the interhemispheric competition and the hemispatial theories. With EEG we recorded brain activity while participants performed an established spatial orienting paradigm (Posner, 1980). In this task, neutral cues provided temporal but not spatially-predictive information, and directional cues prompted covert shifts of visuospatial attention. For both of these attentional states, we quantified alpha power levels in each hemisphere separately and dissociated leftward and rightward shifts of attention. We found that posterior alpha power in the left hemisphere was generally lower than in the right hemisphere and more strongly modulated by neutral (alerting) cues. When isolating the alpha modulation induced by the spatial component of the directional cues specifically, i.e. the modulation induced by spatial attention shifts rather than temporal alerting, we found that the right hemisphere engaged in both leftward and rightward attention shifts, while the left hemisphere engaged in only rightward attention shifts. Below, we discuss how well these results match both the interhemispheric competition and the hemispatial theories.

4.1. Alpha modulation in the absence of spatial information supports the interhemispheric competition theory

The use of a neutral cue condition allowed us to reveal the *baseline* alpha power level, in the absence of spatial attention shifts. Our results show general alpha power differences between the two hemispheres, but also differences in their dynamics, i.e. the change of alpha power during the cue-target interval. Overall, the left hemisphere had lower alpha power compared to the right hemisphere throughout the entire epoch. This result is in line with a previous study that showed similar alpha power differences between hemispheres at rest (Çiçek et al., 2003). The authors suggested that this difference in alpha power might support a dominant role of the right hemisphere in attentional mechanisms and might be related to pseudoneglect, a leftward attentional bias normally

present in healthy subjects (Benwell et al., 2013; Bowers and Heilman, 1980; Schenkenberg et al., 1980). However, it has also been argued that alpha power is inversely related to cortical excitability (Klimesch et al., 2007), so that lower alpha power in the left hemisphere would instead indicate left hemispheric dominance. It is noteworthy that, according to the *interhemispheric competition* theory, left and right hemispheres generate a contralateral bias and are normally kept in balance by mutual inhibition, with the left hemisphere generating a stronger bias (Kinsbourne, 1977). The difference in alpha power we observed between hemispheres might be the electrophysiological marker of the stronger bias the left hemisphere exerts toward the right hemifield, thus supporting the left hemispheric dominance proposed by Kinsbourne.

After the presentation of the neutral cue, a significant decrease of alpha power in both hemispheres was initially driven by the cue-evoked activity but then persisted throughout the entire cue-target interval. Since target stimuli were equally likely to appear in either hemifield in the neutral cue condition, preparation for visual processing is required in both hemifields. It is therefore likely that a bilateral hemispheric engagement takes place by an increase of cortical excitability, thus leading to an alpha activity decrease in both hemispheres. This result is in accordance with previous findings which showed that when a neutral cue is presented, alpha power decreases similarly in the left and right hemispheres (Ikkai et al., 2016). In our case this alpha power decrease was more pronounced in the left hemisphere when computing the relative change from the pre-cue period. Given that alpha power differences between hemispheres were already present prior to the cue, this result needs to be interpreted with caution, but it might reveal interesting nuances in the hemisphere-specific response to a seemingly simple neutral cue that does not convey any spatial information.

4.2. Alpha modulation specific to spatial orienting supports the hemispatial theory

By referencing alpha power of the directional cue conditions to alpha power of the neutral cue condition, in contrast to previous studies, we

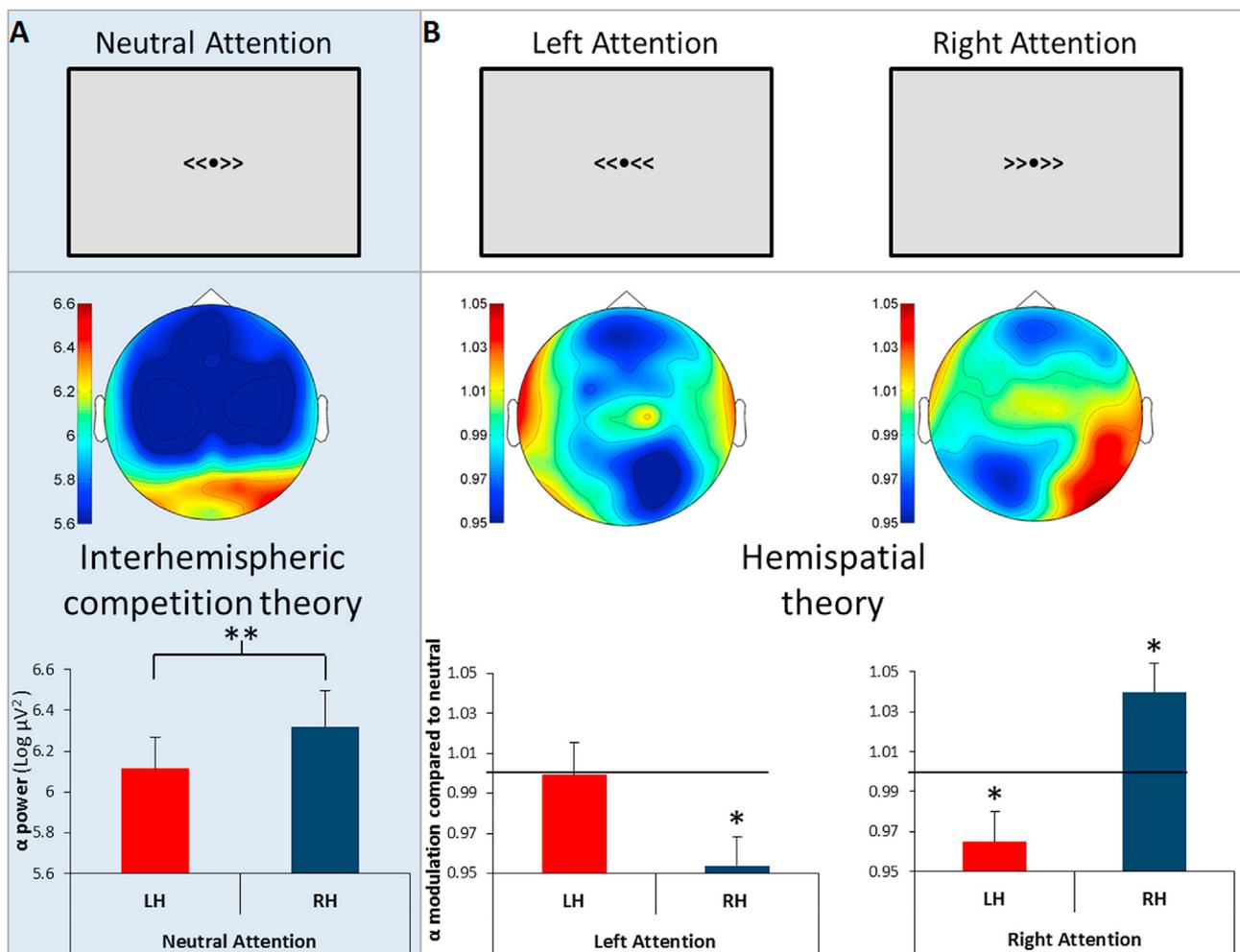


Fig. 4. A). The alpha pattern obtained in response to a neutral cue matches the interhemispheric competition theory. The topoplot shows log-transformed alpha power in response to a neutral cue (no shifts of attention) in the time interval [0.4–1.45 s]. The bar graph shows the same data averaged over time for the left and right occipito-parietal electrodes. The two asterisks represent statistical significance between hemispheres. Error bars represent SEM across subjects. B). The alpha pattern obtained in response to directional cues matches the hemispatial theory. Right attention leads to a contralateral alpha decrease and an ipsilateral alpha increase. Left attention leads to a contralateral alpha decrease and an ipsilateral alpha increase. The topoplots show posterior alpha power modulation in response to directional cues (left and right) as compared to the neutral cue in the time interval [0.4–1.45 s]. The bar graphs show the same data averaged over time for the left and right occipito-parietal electrodes. Bars marked with an asterisk are statistically different with respect to the neutral attention condition ($p < .05$, 1-tail t -test). Error bars represent SEM across subjects.

were able to assess orienting-related alpha modulations in both hemispheres separately. The right hemisphere showed alpha power decreases in response to left attention shifts, as shown previously (Gould et al., 2011; Sauseng et al., 2005; Thut et al., 2006), and in accordance with increased preparatory activity for the attended hemifield. In the case of attention deployed toward the right side, alpha power in the right hemisphere increased. This is in accordance with several studies that showed ipsilateral alpha power increases when attention is shifted toward one side of the visual space (Händel et al., 2011; Jensen and Mazaheri, 2010; Kelly et al., 2006; Worden et al., 2000). Since alpha oscillations have been ascribed an inhibitory function (Hummel et al., 2002; Klimesch et al., 2007), these results suggest that the right hemisphere has a dual role in attention shifts by facilitating the detection of visual stimuli in the contralateral hemifield (by decreasing alpha power), but also inhibiting the influence of irrelevant visual stimuli in the ipsilateral hemifield (by increasing alpha power).

The left hemisphere showed alpha power decreases in response to right attention shifts, mirroring the preparatory activity during contralateral attention shifts observed in the right hemisphere. Critically, alpha power did not increase compared to the neutral condition when shifting attention toward the left side. The left hemisphere seems therefore to be only involved in facilitating detection of visual stimuli in the

contralateral hemifield (by decreasing alpha power), but not in inhibiting irrelevant visual stimuli in the ipsilateral hemifield (absence of alpha power increase). This finding provides a novel insight into the relation between posterior alpha power modulation and attention allocation, showing orienting-related asymmetries not identifiable with attention modulation indexes commonly used.

In sum, the asymmetrical pattern of alpha power modulations observed after directional cues supports a right hemispheric dominance as proposed by the *hemispatial* theory of attention (Heilman & Van Den Abell, 1980), which postulates that the right hemisphere is engaged when shifting attention both toward left and right visual hemifields, but the left hemisphere only in shifting attention toward the contralateral hemifield. Importantly, the lack of alpha power increase in the left hemisphere in response to leftward shifts of attention is in conflict with the interhemispheric competition theory of attention because it postulates an engagement of both hemispheres when shifting attention to either visual hemifield, therefore predicting bilateral alpha power modulation after directional cues. The observed hemispheric asymmetries thus have direct implications for these competing theories of attentional control. Moreover, they also refine our understanding of the functional role of each hemisphere during attention shifts by separating selection and suppression of incoming sensory stimuli thereby clarifying what

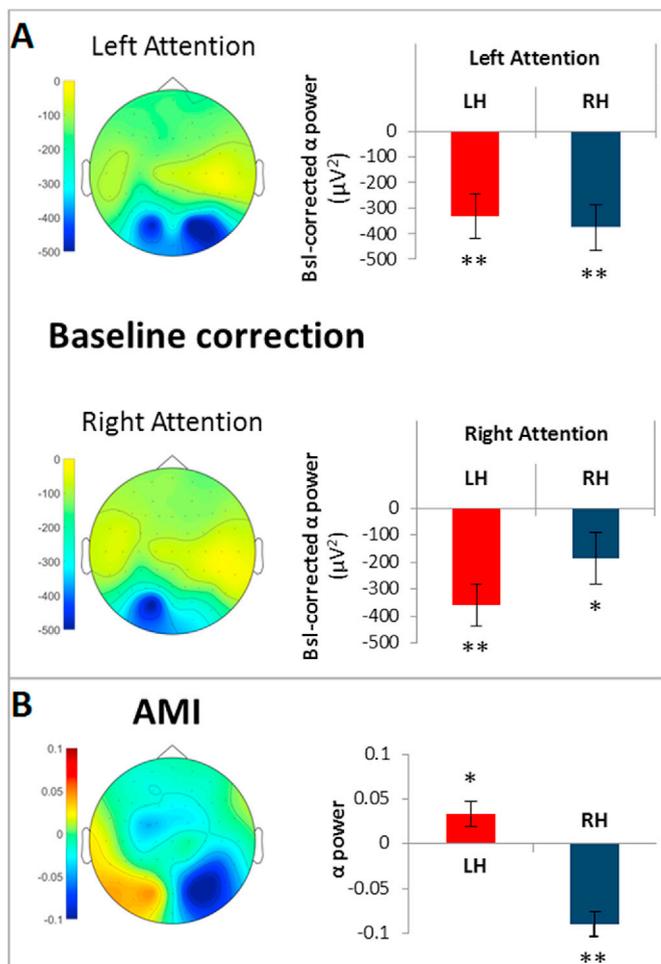


Fig. 5. Alternative normalization approaches. **A)** *Baseline corrected alpha power.* The topoplots show baseline corrected alpha power in response to directional cues (left and right) in the time interval [0.4–1.45 s], baseline period: [-0.65 to -0.25]. The bar graphs show the same data averaged over time for the left and right occipito-parietal electrodes. Error bars represent SEM across subjects. **B)** *Attentional modulation index (AMI).* The topoplots show alpha power in response to right cues subtracted from the alpha power in response to left cues (left – right attention)/(average of left and right attention) in the time interval [0.4–1.45 s]. The bar graphs show the same data averaged over time for the left and right occipito-parietal electrodes. Error bars represent SEM across subjects.

“involvement” of a hemisphere means.

Finally, in the conditions in which alpha power was modulated in response to attention shifts (in the right hemisphere by left and right shifts, in the left hemisphere only by right shifts) the magnitude of change did not differ between hemispheres nor hemifields. This result suggests that when a hemisphere is engaged in shifting attention, its level of engagement is comparable to the other hemisphere, independently of whether it enhances or inhibits stimulus detection. This finding seems to be in contrast with what Ikkai et al. (2016) reported, namely that contralateral attention shifts resulted in greater alpha modulation in the left than in the right hemisphere. They compared alpha modulation of directional cues to a pre-cue period, rather than the neutral cue alpha modulation. Possibly, our approach could reveal these new patterns of hemispheric involvement because it explicitly takes into account task effects shared by directional and non-directional cues.

4.3. Interpretation of the results in the context of a recent functional-anatomical model

The coexistence of the hemispacial and interhemispheric competition

theories was previously proposed in the *hybrid model* of attentional control (Duecker and Sack, 2015). Based on brain stimulation studies, it was argued that distinct hemispheric asymmetries exist in the dorsal attention network. Specifically, the hemispacial theory received strong support by TMS studies targeting frontal regions, whereas the inter-hemispheric theory could account for results of TMS studies targeting parietal regions. Instead of this spatial separation, our findings demonstrate distinct hemispheric asymmetries within parietal cortex depending on the attentional state. Given prior studies showing that attention shifts elicit fronto-parietal coupling within the DAN (Bressler et al., 2008; Buschman and Miller, 2007; Ozaki, 2011; Vossel et al., 2012) with a frontal-to-parietal directionality (Bressler et al., 2008; Ozaki, 2011; Vossel et al., 2012), it seems plausible that the pattern of alpha power modulation observed in parietal cortex is instantiated by top-down signals from frontal cortex. The present findings thus further inform this functional-anatomical model of attention control and highlight the importance of investigating the neurophysiological correlates of distinct attentional states within the dorsal attention network.

4.4. Further considerations

While the inclusion of a neutral cue has been widely used in behavioral studies (see Chica et al., 2014 for a review), a key novelty of the present study is to combine it with electrophysiology, allowing the isolation of orienting-specific alpha power modulations during the cue-target interval for each hemisphere and cue direction separately. Neutral cues elicit many non-directional attention responses, e.g. alerting, arousal, temporal attention, which are thus controlled for in the analyses of alpha responses to directional cues. But one challenge for future studies is to establish what participants actually do during the cue-target interval in the neutral cue condition. They might maintain central fixation without any change in attention, but they might also broaden their focus, divide attention, alternate between hemifields, or even randomly choose a hemifield based on the recent history of trials. None of these task strategies were encouraged by our instructions or rewarded by task progression. Moreover, none of them should systematically affect or confound the current results. But as attention research continues to develop, awareness or empirical assessment of such different task strategies may become a priority, thus improving the control of these factors.

A second intriguing question concerns the functional role of alpha oscillations. While alpha power modulation has been consistently reported in spatial orienting paradigms (Gould et al., 2011; Händel et al., 2011; Rihs et al., 2007, 2009; Sauseng et al., 2005; Thut et al., 2006; Worden et al., 2000), it is not undisputed that they reflect inhibitory processes that gate information processing, as we assume here. A recent line of evidence using simple perceptual tasks suggests that alpha power prior to target appearance may be related to perceptual decision making instead (Benwell et al., 2017; Limbach and Corballis, 2016; Samaha et al., 2017), such as a change in the detection criterion (Iemi et al., 2017). One could thus ask whether alpha power is exclusively related to attentional processes in our task. Irrespectively, as above, the here observed hemispheric asymmetries are of theoretical relevance. But future work should continue to critically address what exact functional contribution alpha power makes across tasks and settings.

Lastly, the hemisphere-specific analysis of alpha power changes conducted here assumes that the topographies roughly correspond to the actual localization of current sources (left versus right hemisphere). There is an abundance of EEG and MEG studies reporting attention-related alpha power changes in the expected hemisphere, i.e., decreases/increases are in agreement with the attended hemifield (Gould et al., 2011; Händel et al., 2011; Kelly et al., 2006; Rihs et al., 2007, 2009; Sauseng et al., 2005; Thut et al., 2006; Worden et al., 2000; Yamagishi et al., 2003, 2005). However, paradoxical lateralization effects have been observed in evoked responses after the presentation of visual stimuli (Barrett et al., 1976; Nakamura et al., 1997). Due to the transversal

orientation of neurons in the parieto-occipital sulcus (Hari and Salmelin, 1997; Vanni et al., 1997), a lateralized visual stimulus may cause EEG signals to be stronger at ipsilateral electrodes and could thus be attributed to the wrong hemisphere. To the best of our knowledge, this has not been demonstrated during the cue-target interval in a spatial orienting paradigm, and MEG studies with state-of-the-art source localization indicate that attention-related alpha oscillation do not originate in such medial brain regions but are more lateralized instead (Händel et al., 2011; Siegel et al., 2008). While we are therefore confident about our interpretation of lateralized effects in this study, it is crucial to keep such source localization challenges in mind.

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Tom A. de Graaf: Formal analysis, Writing – Original Draft, Writing – Review & Editing, Supervision.

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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.2019.116429>.

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