Occipitoparietal alpha-band responses to the graded allocation of top-down spatial attention

Isabel Dombrowe1 and Claus C. Hilgetag1,2
1Department of Computational Neuroscience, University Medical Center Hamburg-Eppendorf, Hamburg, Germany; and 2Department of Health Sciences, Boston University, Boston, Massachusetts

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The aim of our study was to investigate how a graded top-down allocation of attention over the visual field is reflected in the alpha-band activity measured over occipital and parietal cortex and how this compares to a complete attentional shift and evenly balanced attention. To this end, we asked our participants to orient their attention in response to endogenous cues, with a maximal decrease contralateral to the attended hemifield (e.g., Sauseng et al. 2005; Thut et al. 2006). Alpha-band amplitudes relatively lower than at baseline have been linked to better visual performance (Ergenoglu 2004; Hanslmayr et al. 2007; van Dijk et al. 2008; Kelly et al. 2009; Toscani et al. 2010; Foxe and Snyder 2011).

The FEFs have been shown to influence occipitoparietal areas in functional magnetic resonance (fMRI; e.g., Bressler et al. 2008) and transcranial magnetic stimulation (TMS; e.g., Taylor et al. 2007) studies of human participants performing attention tasks. Communication between brain areas such as the FEFs and those within the IPS is assumed to be accomplished by the synchronization of neuronal oscillatory activity (e.g., Fries 2005). In monkeys, this synchronization appears to be mainly in the gamma band (Gregoriou et al. 2009). In humans, a 10-Hz stimulation of the FEFs has repeatedly resulted in a modulation of activity in occipitoparietal areas (Taylor et al. 2007; Hung et al. 2011), suggesting that communication between those areas might be related to synchronization in the alpha-band.

Anatomically, the top-down allocation of visual attention has been linked to activity in regions within the intraparietal sulcus (IPS; Corbetta et al. 2000) and in the frontal eye fields (FEFs; Hopfinger et al. 2000). Sub-saccade-threshold electrical stimulation of the FEFs in the monkey has been shown to increase sensitivity to luminance changes (Moore and Fallah 2004), demonstrating a causal link between the FEFs and attentional selection. In humans, the application of a 10-Hz (i.e., alpha frequency) repetitive transcranial magnetic stimulation (rTMS) on the right FEF has led to diminished top-down attentional control (Hung et al. 2011).

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participants to orient their attention according to three different spatial cues as depicted in Fig. 1A. A 0/100% arrow cue that required a complete shift of attention to one-half of the visual field (i.e., exclusive allocation of attention) and a 50/50% cue that called for a balanced distribution of attentional resources (i.e., equal allocation of attention) represented the boundary conditions. A third cue, a 25/75% arrow, required that participants allocated more attention to one-half of the visual field than to the other (i.e., graded allocation of attention). We probed the allocation of attention by assessing the performance of our participants in detecting a low contrast Gabor that could appear in one-half of the visual field with a probability indicated by the arrow cues.

Recently, Gould et al. (2011) investigated a similar, more specific, question. They asked if the degree of voluntary, top-down allocation of spatial attention would be reflected in a gradual lateralization of the alpha-band amplitudes. They asked their participants to first orient their attention according to one of six different symbolic spatial cues with varying degrees of validity (60, 80, and 100%, left and right, respectively) and then to discriminate the orientation of one of two bilaterally presented Gabors while the EEG was recorded. They analyzed alpha-band amplitudes of the last 200 ms before the first possible time of target onset. They expected the difference between contra- and ipsilateral alpha-band amplitudes to increase with increasing cue validity. Their results were mixed. They found that alpha-band amplitudes lateralized when the 100 and 80% cues were presented but not with the 60% cues, although their participants were clearly faster at responding to validly cued Gabors than to invalidly cued Gabors also with these cues.

In the present study, we asked the more basic question, how a graded top-down allocation of attention is reflected in occipitoparietal alpha-band activity, by contrasting a graded attention condition with an exclusive and an equal condition. Furthermore, we were interested in how alpha-band amplitudes vary over time, during the cueing period and at the time of target onset. Finally, we computed the coherence between frontal and occipitoparietal electrodes for the different conditions as an index of the functional connectivity of occipitoparietal and frontal areas.

**METHODS**

**Participants, Design, and Procedure**

The present study was approved by the local ethics committee (Ethik-Kommission der Aerztekammer Hamburg, Bearb.-Nr. PV4012) and was in compliance with the Declaration of Helsinki.

Eighteen volunteers (3 male) between 18 and 35 yr were paid for their participation. They all reported having normal or corrected to normal visual acuity.

The experiment was implemented using the Psychophysics Toolbox (Brainard 1997) for Matlab (Mathworks, Natick, MA) and run on a Macbook laptop computer (2 GHz CPU, 2 GB RAM) with a Dell 24-in. monitor operating at 60 Hz. Viewing distance was 40 cm. Manual responses were collected with a standard keyboard.

Figure 1B depicts the time course of one trial. Each trial started with the presentation of a fixation cross in the center of the screen and two placeholder squares (6° side length) 15° to the left and right of fixation. Participants were asked to continuously fixate the cross. After a randomly determined time span between 2000 ms and 2,167 ms (jittered cue onset) after fixation display onset, a central arrow cue appeared on the screen. There were three different conditions: Exclu-
sive attention to one-half of the visual field, equal allocation of attention between both hemifields, and graded allocation of attention. Each condition was associated with an arrow cue. First, there was a 0/100% arrow pointing either to the left or the right box. This cue indicated with 100% validity the location of a target Gabor, which would appear in 60 of 84 trials per cue validity condition. Second, a 50/50% arrow cue pointed to both lateral boxes, which was unpredictive of the possible target location. Third, a 25/75% arrow cue with a longer arm pointed to the box in which the target Gabor would appear in 75% of all target present trials and a shorter arm pointed to the box in which the target Gabor would appear with a probability of 25% in all target present trials. The 25% arrow was half as long as the 50% arrow, and the 75% arrow had 75% of the length of the 100% arrow. Trials were presented in random order. Participants could take short breaks after 65, 130, and 195 trials were completed.

Participants were informed about the different probabilities and were asked to distribute their attention accordingly. That is, we explicitly asked them to shift their attention to the indicated side when a 0/100% cue was presented, to distribute their attention evenly between the left and the right placeholder box when a 50/50% cue was presented, and to try and attribute more attention to the side that was indicated with the longer arrow when the 25/75% cue was presented. After 2,000 to 2,167 ms after cue onset (jittered target onset), a target Gabor was presented in 60 of 84 trials of each cueing condition. No target was presented in 24 of 84 trials per cueing condition. The participants’ task was to indicate if a target Gabor had been presented on the current trial by pressing the left or right arrow key for the left and right box, respectively. If the Gabor had been absent on the current trial, participants were asked not to press any keys. Response accuracy was emphasized over response speed. A new trial started after an inter-trial interval of 2 s.

The contrast of the target Gabor was individually determined for each participant by a staircase procedure that was run twice before the start of the experiment. It consisted of randomly determined target present trials, with the Gabor contrast adjusted by the Quest method (Watson and Pelli 1983) using the Quest toolbox for Matlab. The contrast level at which a participant was able to detect 60% of all Gabor presentations was used as the starting contrast. We then determined the contrast level at which a participant was able to detect 60% of all Gabor presentations after an inter-trial interval of 2 s.

To obtain time courses of alpha-amplitude changes during the cue period (see Fig. 4), we averaged relative power changes over all frequencies within the alpha band and over all electrodes within one ROI for three time windows from 0.5 to 1, 1 to 1.5, and 1.5 to 2 s after cue onset. We did not include the first 500 ms in our analysis, since we were not interested in the initial increase in lower frequency power evoked by the physical appearance of the cue.

To obtain alpha-amplitude changes relative to target onset, we reepoched the data and performed time-frequency analyses on the target present trials as described above. We then averaged over alpha-band frequencies (8–14 Hz) in each ROI from 1,000 ms before to 250 ms before target onset to obtain the average alpha power before target presentation.

We computed the coherence between electrodes FC3 and FC4 and all electrodes in both ROIs for the second time window during the cue period and the baseline window using the function ft_connectivity-analysis of the fieldtrip toolbox. This function computes the coherence according to Rosenberg et al. (1989). To compute the alpha-band coherence with a frequency of 11 ± 3 Hz, we extended both time windows by 46 to 546 ms, a window length of six times 90.9090 ms (1,000 ms/11 = 90.9090). This resulted in time windows from 766 to 220 ms before cue onset and 1,000 to 1,546 ms after cue onset. We averaged coherences over the electrodes within each ROI to obtain an index of the functional connectivity between frontal areas such as the FEFs and occipitotemporal areas.

To analyze the participants’ behavioral performance, we calculated the detection sensitivity \(d' = Z(\text{hitRate}) - Z(\text{falsealarmRate})\), where \(Z\) is the inverse of the cumulative Gaussian distribution as well as the accuracy (\%correct) for present targets.

As Fig. 2A depicts, detection sensitivity was better for exclusive \(d' = 2.4\) than for equal allocation of attention \(d' = 1.8, t(13) = 2.88, P = 0.013, 95\%\) confidence interval of the difference (CI) = [0.14 1.01], Bonferroni corrected). Detection sensitivity for graded attention was intermediate \((d' = 2.1)\). Statistically, target detection sensitivity with exclusive and graded attention did not differ \((t(13) = 1.79, P = 0.096, CI = [-0.07 0.71])\), neither did sensitivity with equal and graded attention \((t(13) = 1.81, P = 0.093, CI = [-0.56 0.05])\).

We found the same behavioral pattern for the detection accuracy. Participants detected 80% of all targets with exclusive, 66% of all targets with graded, and 60% of all targets with equal allocation of attention \((\text{all differences significant, Bonferroni corrected}; \text{exclusive vs. graded}: \(t(13) = 3.96, P = 0.0016, CI = [5.18]; \text{graded vs. equal}: \(t(13) = 3.19, P = 0.0071, CI = [2.5 13.2]; \text{exclusive vs. equal}: \(t(13) = 5.01, P < 0.001, CI = [11.1 28])\).

False alarm rates were similar across all three conditions, with a trend towards significance for the exclusive vs. graded conditions. The accuracy of the participants varied across conditions, with a trend towards significance for the exclusive vs. graded conditions.

Electrophysiological Recording and Data Analysis

The EEG was recorded using a 64-channel ActiCap system connected to a BrainAmp MR plus amplifier. Two electrodes usually placed at positions CPz and FCz of the standard 10–10 system were attached to the right and left earlobe, respectively.

We analyzed the EEG data with the FieldTrip toolbox (Oostenveld et al. 2011) for Matlab. The raw data for each subject were epoched after an inter-trial interval of 2 s. The EEG was recorded using a 64-channel ActiCap system connected to a BrainAmp MR plus amplifier. Two electrodes usually placed at positions CPz and FCz of the standard 10–10 system were attached to the right and left earlobe, respectively.

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Electrophysiological Results in the trial.

METHODS. We had to exclude on average 14.2% (SE = 1.7%) of all trials of the graded attention condition, because they contained artifacts. All remaining trials were included in the analysis.

Alpha-band amplitudes during the cue phase. Figure 4 shows the average relative change from the precue baseline for each time window of the three attention conditions. A within-subjects, repeated-measures ANOVA with the factors condition (exclusive, equal, graded), time window (0.5–1, 1–1.5, 1.5–2 s), and ROI (contralateral to the side with a higher target probability, ipsilateral to the side with the higher target probability; in the equal condition left hemisphere electrodes were analyzed as “contralateral” and right hemisphere electrodes as “ipsilateral”) revealed that the three time courses differed [three-way interaction of condition with time window and ROI: F(4,52) = 3.649, P = 0.011]. No other main effects or interactions were significant (all Fs < 2.1, all Ps > 0.1).

Separate ANOVAs for the different conditions showed that the alpha amplitude in the contralateral ROI decreased more relative to the precue baseline than in the ipsilateral ROI when attention was exclusively shifted to one-half of the visual field [interaction of ROI with time window: F(2,26) = 4.462, P = 0.019; see Fig. 4A]. Paired, two-sided t-tests indicated that the difference in alpha-amplitude decrease between ROIs was only significant in the second time window after cue onset (1–1.5 s, t(13) = 2.86, P = 0.013, CI = [−9 1]), Bonferroni corrected.

Behavioral results for the graded allocation of attention condition. As Fig. 3A shows, detection sensitivity was better for targets in the placeholder box that was cued with the 75% arrow than in the box cued with the 25% arrow (2.2 vs. 1.6, t(13) = 3.23, P = 0.0066, CI = [0.20 1.02]). Figure 3B depicts the detection accuracy for present targets in the graded attention condition. Participants detected a greater proportion of targets in the placeholder box that was cued with the 75% arrow (72% of targets detected) than in the box that was cued with the 25% arrow (52% of targets detected, t(13) = 3.32, P = 0.0055, CI = [7 33]). Apparently, they had been following the instructions to attribute more attention to the placeholder box with the higher probability to contain a target later in the trial.

Electrophysiological Results

We analyzed the electrophysiological data as described in METHODS. We had to exclude on average 14.2% (SE = 1.9%) of all trials of the exclusive attention condition, 15.1% (SE = 1.4%) of all trials of the equal attention condition, and 15.1% (SE = 1.7%) of all trials of the graded attention condition, because they contained artifacts. All remaining trials were included in the analysis.

Fig. 2. Behavioral results. A: detection sensitivity (d') for each condition. *P < 0.05, **P < 0.01, significance level for the paired, two-sided t-tests, corrected for multiple comparisons.

Comparison {exclusive attention: 8.6%, graded attention: 5.4%, equal attention: 6%; exclusive vs. graded: t(13) = 2.24, P = 0.043, CI = [0.1 6]; graded vs. equal: t(13) = 0.193, P = 0.85, CI = [−7 6]; exclusive vs. equal: t(13) = 0.987, P = 0.342, CI = [−3 9]; Bonferroni corrected}. However, the observed difference of 3.2% between the exclusive and the graded condition only corresponded to on average 0.768 trials of 24 target absent trials per condition.

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Fig. 3. Behavioral results for the graded allocation of attention condition. A: detection sensitivity (d') for cue validity. B: accuracy for cue validity. **P < 0.01, significance level for the paired, two-sided t-tests.
A separate ANOVA for the equal attention condition did not reveal any main effects or interactions (all \( F < 2.4 \), all \( P > 0.1 \); Fig. 4B).

Critically, there was no difference between ROIs in the graded attention condition. Although participants detected more targets in the box cued with 75% than in the box cued with 25% (Fig. 3B), alpha-band activity did not reflect this behavioral pattern (Fig. 4C).

Two additional ANOVAs comparing only two of the three conditions revealed no main effects or interactions when the equal condition was compared with the graded condition, but a main effect of condition \([F(1,13) = 5.88, P = 0.031]\) and an interaction of condition, ROI, and time window \([F(2,26) = 4.466, P = 0.022]\). This showed that the graded attention condition significantly differed from the exclusive but not from the equal attention condition.

Control analyses. In the following section, we show that the pattern of results described above did not change when we analyzed only the correctly answered trials. Neither did it change when we analyzed absolute alpha-band amplitudes nor when we shortened the time windows to avoid any contamination with activity caused by the onset of the target. Furthermore, we show that the lack of alpha-band lateralization in the graded condition was also not due to systematic eye movements to the expected target location. Finally, we show that baseline alpha-band amplitudes were similar in both ROIs in all three attention conditions.

Correct trials only. We analyzed the correct-trial-only data in the same way as the original dataset containing all trials. Again, we found that the time courses of the three attention conditions differed [three-way interaction of condition, ROI, and time, \( F(4,52) = 4.409, P = 0.004 \), no other significant main effects or interactions, all \( F < 1.6 \), all \( P > 0.2 \)]. Separate ANOVAs of the data of the different attention conditions again showed that the alpha-band amplitudes in the ROI contralateral to the target decreased more relative to the precue baseline than in the ROI ipsilateral to the target when attention was exclusively shifted to one-half of the visual field [interaction of ROI with time window: \( F(2,26) = 4.81, P = 0.033 \)] and that this difference was marginally significant in the second time window from 1 to 1.5 s after cue onset \((t(13) = 2.553, P = 0.024, CI = [−11 −1]) \) but not in the other time windows during the cue phase \((0.5−1 \text{ s}: t(13) = 0.681, P = 0.508, CI = [−6 3]; 1.5−2 \text{ s}: t(13) = 0.523, P = 0.804, CI = [−4 5]; Bonferroni corrected)\]. Again, the ANOVAs for the equal and graded attention conditions did not reveal any significant main effects or interactions.

Absolute alpha-band amplitudes. Absolute alpha-band amplitudes showed a similar pattern to the original, baseline, data.

Although the three-way-interaction of condition, ROI, and time was not significant \([F(2,52) = 1.921, P = 0.121]\), a separate ANOVA of the exclusive attention condition data again showed that the alpha-band amplitude contralateral to the attended hemifield was lower than the ipsilateral amplitude [main effect of ROI: \( F(1,13) = 5.042, P = 0.043 \)]. Paired two-sided \( t \)-tests confirmed that the difference in alpha-band amplitudes was marginally significant in the second time window after cue onset \((1−1.5 \text{ s}: \text{contralateral } 4.9 \mu V^2, \text{ipsilateral } 5.6 \mu V^2, t(13) = 2.519, P = 0.026, CI = [−1.18 −0.09]) \) but not in the other time windows \((0.5−1 \text{ s}: \text{contralateral } 4.7 \mu V^2, \text{ipsilateral } 5.6 \mu V^2)\).

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Fig. 4. Amplitude changes contralateral to the side with the higher target probability are depicted on the left and ipsilateral changes on the right hemisphere. Boxes indicate regions of interest. *\( P < 0.05 \), significance level for the paired, two-sided \( t \)-tests, corrected for multiple comparisons. A: exclusive allocation of attention. Difference between contra- and ipsilateral amplitude changes: 0.5–1 s: mean = −2.5%, SE = 1.89%; 1–1.5 s: mean = −5.26%, SE = 1.84%; 1.5–2 s: mean = −0.04%, SE = 1.82%. B: equal allocation of attention. Difference between contra- and ipsilateral amplitude changes: 0.5–1 s: mean = −2.88%, SE = 2.8%; 1–1.5 s: mean = −0.69%, SE = 2.21%; 1.5–2 s: mean = −1.59%, SE = 2.14%. C: graded allocation of attention. Difference between contra- and ipsilateral amplitude changes: 0.5–1 s: mean = 2.3%, SE = 2.32%; 1–1.5 s: mean = 1.63%, SE = 2.2%; 1.5–2 s: mean = 1.13%, SE = 2.1%.
ipsilateral 4.9 μV², t(13) = 1.846, P = 0.088, CI = [−0.58 0.05]; 1.5–2 s: contralateral 5.6 μV², ipsilateral 5.7 μV², t(13) = 0.689, P = 0.497, CI = [−0.59 0.30]; Bonferroni corrected). Separate ANOVAs of the equal and graded condition data did not reveal any main effects or interactions (all Fs < 2, all Ps > 0.1; absolute power values for the second time window of the graded attention condition were as follows: contralateral to higher target probability 5.5 μV², ipsilateral to higher target probability 5.7 μV², t(13) = 1.419, P = 0.1796, CI = [−0.47 0.10]).

SHORTER TIME WINDOWS. For this control analysis, we first shortened each time window to 280 ms, resulting in windows from 0.5 to 0.78, 1 to 1.28, and 1.5 to 1.78 s after cue onset and then performed an ANOVA with the same factors as in the original analysis. Again, this revealed that time courses of the three attention conditions differed [interaction of condition with time window and ROI, F(4,52) = 2.929, P = 0.029]. A separate ANOVA of the exclusive attention condition data revealed a main effect of ROI [F(1,13) = 5.246, P = 0.039] and a marginally significant interaction of ROI and time window [F(2,26) = 2.837, P = 0.077]. Paired, two-sided t-tests indicated that the difference in alpha-amplitude decrease between ROIs was only significant in the second time window after cue onset [0.5–0.78 s: t(13) = 1.5956, P = 0.1346, CI = [−7.2 1.1]; 1–1.28 s: t(13) = 3.2241, P = 0.0067, CI = [−9.5 −1.9]; 1.5–1.78: t(13) = 0.2899, P = 0.7765, CI = [−4.5 3.4]; Bonferroni corrected]. A separate ANOVA of the data of the equal attention condition showed that the alpha amplitude in the left ROI decreased more than in the right ROI in the first and third but not the second time window after cue onset [matching the pattern depicted in Fig. 4B, marginally significant interaction of ROI and time, F(2,26) = 2.964, P = 0.069]. The follow-up paired t-tests did not reveal any significant differences between contra- and ipsilateral amplitude decreases. A separate ANOVA of the data of the graded attention condition did not reveal any main effects or interactions (all Fs < 1.5, all Ps > 0.2).

EYE MOVEMENTS. To make sure that the lack of alpha-band lateralization in the graded attention condition was not due to systematic eye movements during the cue phase, we obtained eye movement traces separately for each attention condition from electrodes AF7 and AF8 by re-referencing their signals to the midline electrode AFz.

Figure 5, top, depicts the mean voltage changes from electrode AF7, and Fig. 5, bottom, depicts those from electrode AF8. Solid lines indicate voltage changes during trials when the placeholder box with the higher target probability was far from the electrode (i.e., left for electrode AF8 and right for electrode AF7). Dotted lines indicate voltage changes during trials when the placeholder with the higher target probability was near the electrode (i.e., right for electrode AF8 and left for electrode AF7). Different colors denote attention conditions (exclusive: dark gray; graded: light gray; equal: black).

As it can be easily seen in Fig. 5, systematic eye movements, probably to the target location, occurred in the intertrial interval after the target had already disappeared but not during the cue phase. Furthermore, the traces for the exclusive and graded conditions were very similar before and during the time window from 1 to 1.5 s after cue onset. We found alpha-band lateralization during this time window in the exclusive but not the graded attention condition. Thus this difference was probably not caused by different eye movement patterns.
looked at the coherence during the baseline period and the equal attention condition, followed by the exclusive and graded conditions. Since coherence values are not normally distributed, we used paired Wilcoxon signed rank tests for the statistical comparisons. We limited the coherence analysis to the baseline window and the second time window of the cue phase, since we found significant changes in ipsi- and contralateral alpha-band amplitudes during that time.

Fig. 5. Eye movement traces obtained from electrodes AF7 and AF8 by re-referencing to the midline electrode AFz. Solid lines indicate voltage changes during trials when the placeholder box with the higher target probability was far from the electrode (i.e., left for electrode AF8 and right for electrode AF7). Dotted lines indicate voltage changes during trials when the placeholder with the higher target probability was near the electrode (i.e., right for electrode AF8 and left for electrode AF7). Gray tones denote attention conditions (exclusive: dark gray, graded: light gray, equal: black).

Tables 1, 2, 3, and 4 show the coherence values between electrodes FC3/FC4 and both ROIs. Coherence between the right ROI and the frontocentral electrodes was higher than coherence between the left ROI and these electrodes during
The higher coherence with the right ROI was mirrored in the performance of the participants. In the equal attention condition, accuracy for targets presented in the right placeholder box was higher than for targets presented in the left placeholder box (71.9% vs. 47.4%, t(13) = 4.2983, P < 0.001, CI = [0.122 0.369]). This bias to the right was consistent across all conditions (exclusive right: 85.5%, exclusive left: 72.9%, t(13) = 3.2539, P = 0.0063, CI = [0.424 0.210]; graded right: 75.7%, graded left: 59.29%, t(13) = 2.7778, P = 0.0157, CI = [0.037 0.292]). Overall, coherence during the equal allocation of attention was slightly, but not significantly, higher than during baseline (exclusive: 0.54, baseline: 0.50, Z = −1.85, P = 0.064, difference range −0.04 – 0.17).

When attention was exclusively allocated to the right half of the visual field, coherence of the right ROI with the frontocentral electrodes was higher than coherence with the left ROI (right: 0.57, left: 0.44, Z = −3.3, P < 0.001, difference range 0.01 – 0.30). This difference was reversed when attention was allocated to the left half of the visual field (right: 0.42, left: 0.58, Z = −3.3, P < 0.001, difference range −0.27 to −0.01, all tests Bonferroni corrected).

Results were similar when attention was graded. When the longer side of the arrow cue pointed to the right, coherence with the right ROI was higher than with the left ROI (right: 0.57, left: 0.44, Z = −3.3, P < 0.001, difference range 0.01 – 0.24). This pattern again reversed when the longer side of the arrow cue was pointing to the left side (right: 0.41, left: 0.57, Z = −3.3, P < 0.001, difference range −0.34 to −0.01, all tests Bonferroni corrected).

It is important to note that one should not interpret the absolute coherence values listed in Tables 1–4. Since we computed the coherence at the sensor level and not at the source level, our electrodes of interest (FC3/4, occipitoparietal ROI electrodes) recorded signals from one or more sources located anywhere within the brain. However, we can assume that the location of these sources should have been quite stable across the three attention conditions, as the tasks (i.e., attention equally to both sides, attend to one side, attend more to one side) were very similar to each other. This similarity was also reflected in the amplitude results reported above. Furthermore, one should keep in mind that coherence increases could simply be caused by amplitude increases in one or more sources. A coherence increase between frontal and occipitoparietal areas ipsilateral to the (main) cue direction could therefore be due to a lateralized alpha-band amplitude increase at the source level, which was not detected at the sensor level. However, since we observed an alpha-band coherence increase from baseline to

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**Table 1. Baseline coherence**

<table>
<thead>
<tr>
<th>ROI</th>
<th>Left ROI</th>
<th>Right ROI</th>
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</thead>
<tbody>
<tr>
<td>FC3</td>
<td>0.43</td>
<td>0.59</td>
</tr>
<tr>
<td>FC4</td>
<td>0.44</td>
<td>0.55</td>
</tr>
</tbody>
</table>

ROI, region of interest. FC3 and FC4, electrodes.

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**Table 2. Equal allocation of attention: coherence**

<table>
<thead>
<tr>
<th>ROI</th>
<th>Left ROI</th>
<th>Right ROI</th>
</tr>
</thead>
<tbody>
<tr>
<td>FC3</td>
<td>0.44</td>
<td>0.63</td>
</tr>
<tr>
<td>FC4</td>
<td>0.48</td>
<td>0.59</td>
</tr>
</tbody>
</table>

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Fig. 6. Relative changes in alpha-band amplitudes for regions of interest contralateral and ipsilateral to the target. Left: amplitudes when the target was detected. Right: amplitudes when the target was undetected. A: exclusive allocation of attention. B: equal allocation of attention. C: graded allocation of attention. *P < 0.05, **P < 0.01, significant differences from zero by one-tailed t-tests, corrected for multiple comparisons. Error bars indicate ±1SE.
cue phase, while the alpha-band amplitudes decreased, a major contribution from amplitude increases to the observed coherence seems unlikely.

DISCUSSION

In the present study, we investigated occipitoparietal alpha-band responses to the allocation of exclusive, equal, and graded top-down spatial attention. We found that when attention was shifted exclusively to one-half of the visual field, contralateral alpha-band amplitudes decreased more than ipsilateral alpha-band amplitudes, until they were maximally different in a time window from 1 to 1.5 s after the onset of a spatial cue. This alpha-band lateralization disappeared in the following and last time window before target onset. When attention was allocated equally across the visual field, occipitoparietal alpha-band amplitudes decreased bilaterally below baseline level and remained constant throughout the cue period. Although the behavioral results showed that participants allocated more attention to one-half of the visual field in the graded attention condition, we did not find this reflected in the occipitoparietal alpha-band amplitudes. Similar to the equal attention condition, alpha-band amplitudes decreased below baseline in both ROIs.

We further found that occipitoparietal alpha-band amplitudes in the hemisphere contralateral to the target were significantly lower than at baseline when a target was detected but not when a target was missed.

Moreover, we found that coherence between frontal and occipitoparietal regions was stronger in the hemisphere ipsilateral than in the hemisphere contralateral to the (main) cue direction when attention was attributed exclusively or graded. Coherence only slightly increased overall when attention was balanced equally across the visual field.

Our study differs from most other studies that used cues with a validity lower than 100%, in that we instructed our participants to try to distribute their attention according to the target probabilities indicated by the cue. In the majority of related studies, participants were instructed to exclusively shift their attention toward the side with the higher target probability, e.g., in the studies of Thut et al. (2006; 66%), Rihs et al. (2009; 75 and 95%), and Sauseng et al. (2011; 75%). With the instruction to exclusively attend to the side with the higher target probability, alpha-band lateralization will probably occur naturally despite a graded cue.

Our results indicate that alpha-band amplitudes measured over the occipitoparietal cortex do not necessarily reflect how attention is allocated across the visual field. If the absolute magnitude of amplitude decrease from baseline indexed how much attention was allocated to a part of the visual field, we should have observed a maximal decrease contralateral to the side cued with 100%, followed by the decrease contralateral to the 75% side, followed by 50% and finally 25%. However, this is not what we observed. We also did not find it reflected in the relative contra- and ipsilateral amplitudes, such that the allocation of more attentional resources to one-half of the visual field resulted in a more pronounced contralateral decrease from baseline amplitudes compared with ipsilateral amplitudes. We also did not find it reflected in the difference between contralateral and ipsilateral amplitudes, as suggested by Gould et al. (2011).

We did find, however, a clear lateralization of alpha-band amplitudes with a lower contralateral amplitude than ipsilateral when attention was exclusively shifted to one-half of the visual field. This is in line with previous studies that asked participants to covertly shift their attention away from fixation into one-half of the visual field (Sauseng et al. 2005, 2011; Thut et al. 2006; Rihs et al. 2009; Cosmelli et al. 2011). Rihs et al. (2009) observed an alpha-band lateralization driven by lower contralateral than ipsilateral amplitudes during the first 700 ms after cue onset, which turned into a lateralization driven by ipsilateral amplitude increases during the later cueing phase when attention was presumably held at the new location. Although we did not observe a switchover, the absence of alpha-band lateralization in the later cueing phase might reflect that participants had already completed the shift of attention and were now waiting for the target onset with their attention focused on the cued placeholder box. A possible reason for this fast attentional switch might be that we used cues that indicated the side of the target with 100% validity and that we did not present a distracter along with the target. This allowed our participants to swiftly reorient their attention to the side of the upcoming target without having to consider possible targets or distracters elsewhere on the screen.

In the absence of a clear correlate of graded attention in the alpha-band amplitudes measured over the occipitoparietal cortex, what might be other physiological mechanisms that can explain the behavioral effects of our study? It has been shown that occipitoparietal alpha-band activity is modulated by top-down inputs from frontal areas, such as the FEF, when covert visual attention is voluntarily allocated to a location in the visual field (Taylor et al., 2007; Capotosto et al. 2009; Sauseng et al. 2011). Indeed, we found an indication for such a modulation in an increased coherence between our ROIs and frontal electrodes above the FEFs when attention was exclusive and graded. When attention was attributed equally across the visual field, coherence increased only slightly relative to baseline.

Conclusion

We conclude that occipitoparietal alpha-band amplitudes lower than baseline seem to be a necessary precondition of visual stimulus detection. At least according to the results of our study, other factors, such as coupling between frontal and posterior cortices, might be more likely to reflect how spatial attention is allocated across the visual field than the absolute or relative alpha-band magnitudes measured over the occipitoparietal cortex.

Table 3. Exclusive allocation of attention: coherence

<table>
<thead>
<tr>
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Table 4. Graded allocation of attention: coherence

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<th>Left ROI</th>
<th>Right ROI</th>
</tr>
</thead>
<tbody>
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<td>FC3</td>
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<td>0.42</td>
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</tr>
<tr>
<td>FC4</td>
<td>0.56</td>
<td>0.42</td>
<td>0.45</td>
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</table>
ACKNOWLEDGMENTS
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DISCLOSURES
No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS
Author contributions: I.D. conception and design of research; I.D. performed experiments; I.D. analyzed data; I.D. and C.C.H. interpreted results of experiments; I.D. prepared figures; I.D. drafted manuscript; I.D. and C.C.H. edited and revised manuscript; I.D. and C.C.H. approved final version of manuscript.

REFERENCES