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Spatial Attentional Selection Modulates Early Visual Stimulus Processing Independently of Visual Alpha Modulations

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Abstract

The capacity-limited human brain is constantly confronted with a huge amount of sensory information. Selective attention is needed for biasing neural processing towards relevant information and consequently allows meaningful interaction with the environment. Activity in the alpha-band has been proposed to be related to top-down modulation of neural inhibition and could thus represent a viable candidate to control the priority of stimulus processing. It is, however, unknown whether modulations in the alpha-band directly relate to changes in the sensory gain control of the early visual cortex. Here, we used a spatial cueing paradigm while simultaneously measuring ongoing alpha-band oscillations and steady-state visual evoked potentials (SSVEPs) as a marker of continuous early sensory processing in the human visual cortex. Thereby, the effects of spatial attention for both of these signals and their potential interactions were assessed. As expected, spatial attention modulated both alpha-band and SSVEP responses. However, their modulations were independent of each other and the corresponding activity profiles differed across task demands. Thus, our results challenge the view that modulations of alpha-band activity represent a mechanism that directly alters or controls sensory gain. The potential role of alpha-band oscillations beyond sensory processing will be discussed in light of the present results.

Key words: alpha oscillations, EEG, spatial attention, steady-state visual evoked potentials, vision

Introduction

The visual system is constantly confronted with continuous and ubiquitous input. Perception as a constituent element of successful and meaningful interaction with the environment relies on the selection of relevant information. Selective visual attention as the key function to prioritize relevant information over irrelevant information has been vastly studied (see [Carasco 2011](#) for a review). Traditional attentional models posit information bottlenecks resulting in attentional selection either at an early or late perceptual stage ([Broadbent 1958](#); [Deutsch and Deutsch 1963](#); [Treisman 1964](#); [Lavie and Tsal 1994](#)). Attentional

selection of a particular stimulus location or stimulus feature has been shown to modulate neural activity at early sensory processing levels. Attended locations or features usually generate increased neural responses ([Corbetta et al. 1990](#); [Morgan et al. 1996](#); [Hillyard et al. 1998](#); [Hopfinger et al. 2000](#); [Müller and Hillyard 2000](#)), whereas unattended locations or features result in a suppression of neural responses ([Moran and Desimone 1985](#); [Kastner and Ungerleider 2001](#); [Martinez-Trujillo and Treue 2004](#); [Reynolds and Heeger 2009](#); [Andersen and Müller 2010](#)). These observations have been conceptualized as “sensory gain” modulation by attentional filtering. However, despite a vast

literature on attentional selection, it is not fully understood how the brain implements attentional filtering mechanisms as reflected by sensory gain modulations. More importantly, it is unknown at which stage(s) of the processing stream this mechanism is instantiated.

Synchronization or desynchronization of oscillatory neural activity in the alpha-band (8–12 Hz) might be one way how the brain gates attentional selection on the neural level. One notion is that synchronized alpha-band oscillations inhibit and desynchronized alpha-band activity excites sensory cortical areas (or at least reflects these processes). Thereby, top-down modulated alpha-band activity may serve as a neural mechanism to suppress behaviorally irrelevant and facilitate relevant information (cf. Klimesch et al. 2007; Jensen and Mazaheri 2010; Foxe and Snyder 2011). Indeed, a number of studies using attentional (spatial) cueing paradigms showed that alpha-band responses were increased in amplitude for the to-be-ignored as compared with the to-be-attended location consistent with behavioral performance (Worden et al. 2000; Sauseng et al. 2005; Kelly et al. 2006; Thut et al. 2006; Rihs et al. 2007; Capotosto et al. 2009; Gould et al. 2011; Capilla et al. 2014; Frey et al. 2014; Ikkai et al. 2016; Feng et al. 2017; Foster et al. 2017; Green et al. 2017; Popov et al. 2017; Voytek et al. 2017; Heideman et al. 2018). These studies were complemented by studies that linked prestimulus fluctuations in alpha power to altered perception; again in line with an inhibitory account, high prestimulus alpha power was accompanied by degraded visual perception (Ergenoglu et al. 2004; van Dijk et al. 2008; Busch et al. 2009; Mathewson et al. 2009; Romei et al. 2010; Chaumon and Busch 2014; Limbach and Corballis 2016; Benwell et al. 2017; Iemi et al. 2017; Samaha et al. 2017).

While these findings render alpha modulations a promising candidate for modulating perceptually relevant neural processing, it is under debate whether it indeed represents an active mechanism (or is just an epiphenomenon of a latent process). Crucially, it is still unclear at which processing level these alpha-band modulations are implemented. Foxe and Snyder (2011) initially proposed alpha oscillations to be an active suppression mechanism reflecting top-down spatial attention that alters cortical stimulus representations from early processing stages onwards (i.e., that alters sensory gain and, thus, acts as a sensory gain control mechanism). More recent studies, however, found alpha modulations to be presumably more relevant for later processing stages as they co-varied with response criterion shifts (Limbach and Corballis 2016; Iemi et al. 2017), decision confidence (Samaha et al. 2017), and awareness of visual experiences (Benwell et al. 2017; Iemi and Busch 2018) rather than the sensitivity in visual discrimination tasks. Crucially, most of these studies relied on behavioral measures, and never have examined (see Foxe and Snyder 2011) nor challenged (see Chaumon and Busch 2014 for instance) the proposed mechanistic role of alpha activity in the modulation of early sensory processing.

Furthermore, a closer inspection of electrophysiological spatial attention studies (EEG/MEG) reporting on alpha-band modulations by attention reveals that alpha-band responses were rarely analyzed under conditions of visual stimulation but were restricted to stimulus free time periods, such as the interval between a spatial cue and the following stimulus. Such designs render the analysis of alpha-band modulations under ongoing spatial attentional selection and its impact on early levels of stimulus processing questionable. Only a few studies investigated the temporal dynamics of alpha-band responses with concurrent visual stimulation in a spatial attention paradigm

(see for instance: Kelly et al. 2006; Händel et al. 2010). Unfortunately, these studies only focused on the analysis of alpha-band responses and neglected the analysis of neural responses that were elicited by the respective stimuli. However, to test if modulations in oscillatory alpha-band activity reflect the active inhibition or facilitation of the to-be-ignored or to-be-attended stimulus, respectively, neural dynamics of alpha-band and early stimulus-evoked responses have to be analyzed concurrently for the same participants. Therefore, in the present study, we will fill that conceptual gap by analyzing alpha-band and stimulus-locked steady-state visual evoked potential (SSVEP) modulations during cued spatial attention shifts. SSVEPs are neural markers of ongoing early visual cortex activity evoked by continuously presented flickering stimuli (Regan 1989; Hillyard et al. 1997; Müller et al. 2006; Di Russo et al. 2007). Attentional SSVEP amplitude changes reflect early sensory gain control mechanisms, similar to what has been reported for the transient P1 and N1 components of the visual evoked potential (cf., Hillyard et al. 1998; Müller and Hillyard 2000). In the present study, participants were cued to shift attention to one of the flickering stimuli in the left or right visual hemifield in a trial-by-trial fashion. Critically, the attentional focus during the pre-cue period (either towards or away from both stimuli) was also controlled. This allows examining alpha-band and SSVEP amplitude modulations under the control of the attentional focus during physically identical pre-cue baseline intervals for the same participants.

We hypothesized that, if alpha oscillations were a mechanism of top-down gating of spatial attention that directly alters early sensory gain, the increase of ipsilateral alpha-band activity (with respect to the to-be-attended hemifield) would predict a decrease of ipsilateral SSVEP responses. Consequently, a decrease of contralateral alpha amplitude would predict an increase of contralateral SSVEP responses. Critically, alpha-band amplitude changes would have to precede SSVEP amplitude modulations in time after spatial cue onset. Importantly, a negative correlation between alpha-band and SSVEP amplitude modulations should not only be observed across participants but also across trials within participants. Finally, we expect stronger inhibitory dynamics of alpha-band activity on SSVEP responses when both hemifields have to be attended during the pre-cue period.

Materials and Methods

Participants

About 20 participants (13 female; mean age: 22.2; age range: 18–33) took part in the experiment and received either class credits or financial reimbursement for participation. Based on previous findings on the effects of covert spatial attention on SSVEPs (cf., Müller, et al. 1998a; Walter et al. 2012) as well as visual alpha-band responses (Capilla et al. 2014), we calculated the required sample size with a power ($1-\beta$ error probability) of 0.8 and an α error probability of 0.05 using G*Power (Faul et al. 2009). The calculated required minimum sample sizes ranged between 6 and 14, so we reasoned 20 subjects to be of adequate size to study the potential interaction of both effects in a within-subject design. All participants had normal or corrected-to-normal vision. Prior to the study, participants gave written informed consent and were informed about the nature of the experiment. The study was designed and conducted according to the declaration of Helsinki and the local ethics committee.

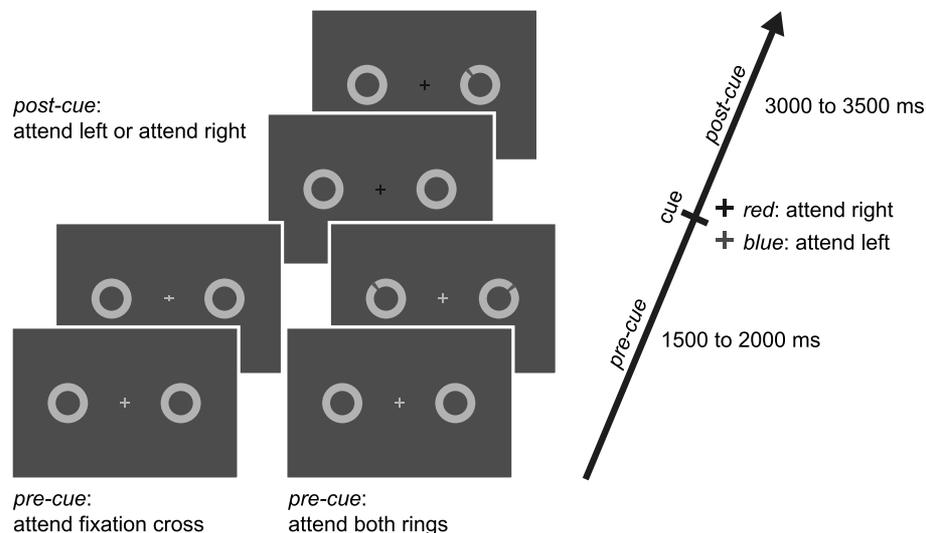


Figure 1. Stimulus display. Each trial lasted between 4500 and 5500 ms and was divided into a pre-cue period and a post-cue period. During the pre-cue period, participants either had to detect brief decreases in the size of one of the lines of the fixation cross (attend fixation cross) or had to detect brief decreases in the luminance of small arcs at the left and right ring (attend both rings). For the post-cue period, luminance decreases had to be reported for the cued side. The to-be-attended side was cued by a color change of the fixation cross to either red or blue. A target event for each pre-cue task and the post-cue task is shown. Note: not to scale.

Stimuli

Stimuli were created with custom scripts using the Psychophysics Toolbox 3 (Brainard 1997; Kleiner et al. 2007) implemented in Matlab 7.5 (The MathWorks) running in a Windows XP (Microsoft Corporation) environment and were presented on a 19-inch CRT monitor set to a resolution of 1024-by-768 pixels, color depth of 32 bits, and refresh rate of 85 Hz situated 80 cm away from the subject. The stimulus display consisted of two rings with an outer and inner diameter of 4.6 and 2.8° of visual angle presented 6.4° left and right to a centrally presented fixation cross of size 0.38° by 0.38° with a width of 0.08° of visual angle (see Fig. 1). Both rings were presented on a gray background (luminance of 13 cd/m²) with an on-off flicker of 14.167 Hz for the left and 17 Hz for the right stimulus, having a luminance of 60 cd/m² during the on frames. Fixation cross target stimuli were decreases of either vertical or horizontal length by 0.25–0.127° in visual angle, while distractors were increases in the size of the same magnitude presented for 100 ms. Events for the rings were 150-ms long decrease in the luminance of an arc measuring 8° (appearing as a stripe within in the ring), which was presented at any position of the ring with a light decrement of 8 to 23 cd/m².

Experimental Procedure and Task

Following the electroencephalographic (EEG) preparation, participants were seated comfortably in an electromagnetically shielded and acoustically damped chamber. The experiment consisted of a spatial attention paradigm implementing a speeded reaction time task. Each trial of the spatial attention paradigm consisted of two periods with different subtasks as shown in Figure 1.

During the “pre-cue” period of each trial, participants performed either a detection task at the fixation cross to focus attention to the center of the screen or a detection task at both rings to split and extend spatial attention to the left and right

visual hemifields simultaneously. For the “fixation cross” task, brief decreases in either the horizontal or vertical dimension of the cross had to be detected and reported (target), whereas increases had to be ignored (distractor). For the “both rings” task, simultaneous decreases in the luminance of arcs in the left and right rings had to be detected and reported (target), while single events in one visual hemifield had to be ignored (distractor). For both tasks, pre-cue periods contained either none or one event occurring with the same probability. Furthermore, targets appeared as likely as distractors and both events were presented randomly in a time window starting 300 ms after trial onset and ending 500 ms before the spatial attentional cue was presented and the post-cue task started (see below).

After 1500–2000 ms, the fixation cross changed color to either red or blue indicating that either the left or right stimulus needs to be attended henceforth (the assignment of side and color was counter-balanced across subjects). During this post-cue time window (duration between 3000 and 3500 ms), participants had to detect and report brief decreases in the luminance of arcs of the to-be-attended ring with a button press while ignoring such events at the to-be-ignored side. Half of the post-cue time windows contained no events, whereas the other half had up to two events, separated by at least 800 ms and distributed randomly across the central part of the post-cue time window (300 ms after cue onset to 500 ms before trial end). Targets were as likely as distractors (i.e., events at the uncued side). Trials were separated by a jittered intertrial interval of 1500–2000 ms, during which only the fixation cross was presented and which served as the time window to allow subjects to blink.

For both pre-cue tasks and the post-cue task, the detection of targets had to be reported with a press of the space bar with either the left or right hand. The responding hand (left or right) was instructed before the onset of each block and quasi-randomized across blocks.

The experimental factors PRE-CUE TASK (attend fixation cross vs. attend both rings) and POST-CUE ATTENTION (attend left vs. right) were fully balanced. About 120 repetitions for each

condition resulted in a total trial number of 480 presented in 10 blocks, each lasting around 6 min. The type of pre-cue task was kept constant within each block (sequence randomized across subjects), and subjects were informed on the specific pre-cue task before each block. After each block, the average hit rate and response time for the pre- and post-cue time window were presented as feedback. The experiment started with a short training to familiarize subjects with the stimulus display and task.

Behavioral Analysis

Button presses that occurred between 200 and 1000 ms after the onset of an event (target or distractor) were considered as hits or false alarms.

Electrophysiological Data Recording

EEG was measured from 64 Ag/AgCl electrodes mounted in an elastic cap with an ActiveTwo Amplifier (BioSemi) at a sampling rate of 256 Hz with a high-pass filter of 0.16 Hz and a low-pass filter of 100 Hz and stored for later offline analysis. Two electrodes were placed horizontally at the canthi of both eyes and vertically above and below the right eye to measure horizontal and vertical eye movements as well as blinks.

Preprocessing of Electrophysiological Data

For offline data analysis, the EEGLAB toolbox (Delorme and Makeig 2004) and custom MATLAB scripts (The MathWorks) were used. In the first step, the continuous data were epoched from –2500 to 4000 ms relative to cue onset. These epochs were larger than the relevant time window (–1500 to 3000 ms) to prevent edge artifacts of following Gabor-filter-based analyses in the relevant time window (see below). Subsequently, for the relevant time window (–1500 to 3000 ms), different generators and sources of artifacts were identified and corresponding data discarded or interpolated; after linear trends were removed, trials containing blinks and/or eye movements were discarded, based on an adaptive threshold procedure for blinks (average number of trials discarded per subject, $M = 30.000$; $SD = 33.219$) and eye movements (average number of trials discarded per subject, $M = 98.500$; $SD = 59.509$). Subsequently, the “statistical control of artifacts in dense array EEG/MEG studies” (Junghofer et al. 2000) was applied. Derived from statistical parameters of the data, channel data were either interpolated, or in case of noise contamination of more than 15 data channels in each trial, trials were rejected. On average, 3,490 channels were interpolated per trial ($SD = 0.903$). The long trial length of 4500–5000 ms, together with a demanding visual detection task containing a shift in spatial attention, required a conservative selection of trials in order to control for eye movements. Overall, 19,850 trials were rejected on average ($SD = 20.789$), and thus, on average, 89,488 trials entered the analysis ($SD = 17.991$) for each experimental condition (fixation cross and attend left: $M = 91.950$, $SD = 16.579$; fixation cross and attend right: $M = 91.3$, $SD = 17.433$; both rings and attend left: $M = 88.850$, $SD = 18.945$; both rings and attend right: $M = 85.850$, $SD = 19.009$). For all subsequent analyses, trials with pre- and post-cue events were included. As the design of the event parameters was fully balanced and orthogonal to the main experimental factors, any contribution of dynamics related to the perception of and response to events was minimized (see Supplemental Results for a quantitative estimation).

Subsequently, preprocessed data were transformed to reference-free scalp current densities (SCDs), to allow for better assessment of sources from scalp potential amplitude topographies with more distinct maxima (Ferree 2006; Kayser and Tenke 2006; Kayser 2009; Müller et al. 2018).

Analysis of Electrophysiological Data

The aim of the analysis of electrophysiological data was to examine the relationship between early sensory gain (as indexed by SSVEPs) and neural alpha-band responses during sustained stimulus processing at a certain location.

Temporal Dynamics of Attentional Modulation of SSVEPs and Alpha Oscillations

In an initial step, the temporal dynamics of attentional modulations of SSVEP and alpha-band amplitudes were analyzed. For this purpose, the time courses for the left and right SSVEP and alpha-band responses were extracted from the CSD-transformed single-trial data for each condition, channel, and subject, using a Gabor-filter-based transformation of the data (bandwidth of filter: $FWHM_{\text{frequency}} = \pm 1$ Hz; $FWHM_{\text{time}} = \pm 220.636$ ms). For both SSVEPs, a Gabor filter for the exact stimulation frequencies (14.167 and 17 Hz, respectively) was constructed to extract their time courses. For the extractions of alpha-band oscillations, multiple single Gabor filters were constructed with frequencies from 8 to 12 Hz in 0.25 Hz steps and the multiple time courses subsequently averaged to yield a single alpha-band time course. By using the same Gaussian kernel for constructing the Gabor filters for all estimated frequency responses, the time and frequency resolutions for the time courses of SSVEP and alpha-band oscillations were exactly the same. SSVEP and alpha-band time courses were extracted from central and lateral electrode clusters (see Fig. 2). Electrodes that were entered into the analysis were identified as those with the largest grand mean amplitude values averaged across all conditions and time windows. The selected electrode clusters were the same for all participants and all subsequent analyses and are highlighted in Figure 2; for the extraction of the SSVEP time series, a right-lateralized electrode cluster contralateral to attend left hemifield contained 10 electrodes (POz, Oz, Iz, PO4, O2, I2, PO8, P6, P8, and P10), and a mirror-symmetric left electrode cluster was selected for the attended right hemifield (POz, Oz, Iz, PO3, O1, I1, PO7, P5, P7, and P9). The right alpha-band cluster (contralateral to the left stimulus) contained seven electrodes (PO4, O2, I2, PO8, P6, P8, and P10), and mirror-symmetrically left alpha cluster (contralateral to the right stimulus) contained PO3, O1, I1, PO7, P5, P7, and P9. For the analysis of central alpha responses electrodes, POz and Pz were selected. Amplitude time courses extracted from these clusters were normalized according to the following formula:

$$A_{\text{norm}}(t) = \left(\frac{A(t)}{\bar{\chi}_{\text{Grandmean}}(t_{\text{pre-cue}})} - 1 \right) * 100. \quad (1)$$

Here, $A(t)$ represents amplitude values at each time point, and $\bar{\chi}_{\text{Grandmean}}(t_{\text{pre-cue}})$ represents the grand mean pre-cue amplitude value (from –1000 to –220.636) averaged across all conditions. We discarded a period of 220.636 ms previous to the cue to avoid the inclusion of post-cue data, due to temporal smearing of the Gabor filter. Amplitude values were thus represented as the differences in percent from an

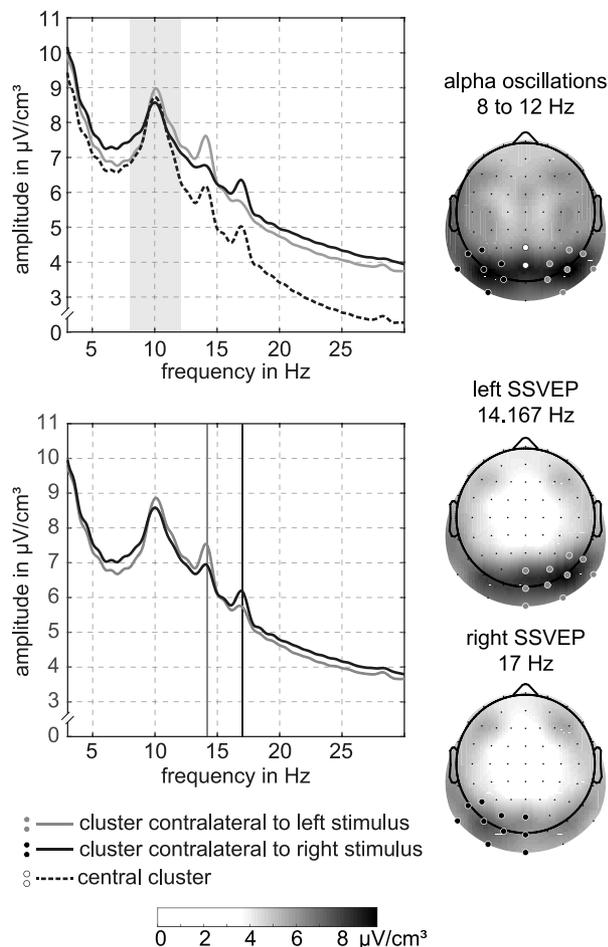


Figure 2. FFT-spectra and topographies of alpha-band responses and SSVEPs. The FFT amplitude spectra for alpha-band responses (top) and SSVEPs (bottom) are shown separately for data from the corresponding electrode clusters. The alpha-band range (8–12 Hz) is shaded in gray. SSVEP frequencies are marked by vertical lines (gray = left stimulus; black = right stimulus). Next to the spectra topographies of grand mean, FFT derived amplitude values, averaged across all conditions and the pre- and post-cue time window, are shown. Electrodes for each electrode cluster, used for all analyses, are marked. Black marks define the electrode cluster contralateral to right and gray contralateral to left stimulus, and white marks the central electrode cluster.

experimentally controlled pre-cue amplitude, representing the average across all conditions. For each subject and condition, the time courses were then averaged across trials and pooled across the left and right hemisphere to represent alpha and SSVEP amplitudes contralateral to the attended and unattended stimulus independently of whether it was presented on the left or right side. Note that signals labeled as “contralateral to the unattended stimulus” are equivalent to signals “ipsilateral to the attended stimulus.” Thus, we ended up with four time-courses of SSVEP and alpha amplitudes that represented the combination of our experimental factors PRE-CUE TASK (“attend fixation cross” or “both rings”) and POST-CUE ATTENTION, i.e., alpha and SSVEP signals representing the stimulus that became attended versus unattended in the post-cue task, respectively. Additional time courses for alpha responses were calculated for central electrodes in the same manner.

In order to relate the temporal dynamics of lateral alpha oscillations and SSVEPs, we first calculated a running paired

t-test that sequentially compared each post-cue data point to the pre-cue reference amplitude (i.e., averaged across the pre-cue time window from -1000 to -220.636 ms) for each signal and condition. As a very conservative approach, we discarded the first 500 ms after the cue from these running t-tests to avoid the contamination of both alpha and SSVEP amplitudes by the evoked potential that was elicited by the cue (see also Kelly et al. 2006, for a more extended period). As shown in Figure 3A, the cue related P1/N1 component of the ERP has power in the frequency bands of interest, in particular within the alpha band (see the peak around time point zero). A second reason to exclude that time window from the running t-tests is the time attention needs to be shifted to the cued location, estimated in previous spatial shifting experiments at about 500 ms (Müller, et al. 1998b; Müller 2008). This yielded time points for which SSVEP and alpha oscillations were modulated significantly after the cue as compared with the pre-cue baseline separately for each condition. The results of the running t-tests were cluster-corrected with a cluster mass approach as suggested by Bullmore et al. (1999) and Maris and Oostenveld (2007). The procedure in brief: P-values of point-by-point statistical tests were thresholded at $P < 0.05$. T-values for each significant cluster (i.e., a sequence with significant data points) were then summed. These t-sum values were compared with a resampled surrogate distribution of random t-values created by repeating the same analysis 10 000 times whereby condition labels were shuffled, and thus any dependency on experimental conditions was abolished.

In order to directly relate the onset times of post-cue attentional dynamics between alpha-band and SSVEP amplitude time courses, single-subject onset time points were estimated via a jackknifing procedure (Ulrich and Miller 2001; Smulders 2010). In brief, 20 jackknife subsamples of data with $N-1$ subjects were created by leaving out one single subject turn by turn. For each subsample, the average amplitude time courses for both SSVEP and alpha-band oscillations and conditions were calculated as described above. Based on these subaverages, for all signals and conditions for which a significant post-cue modulation was found in the whole sample as described above (see results), the onset time of these modulations was estimated for each of the subsamples. The onset time was operationalized as the time point when the amplitude in a post-cue time window (500–3000 ms) reached 50% of the average amplitude modulation from pre-cue (-1000 to -220.636 ms) to post-cue (1000–3000 ms) derived from the whole sample ($N = 20$). From these sets of sub-average onset times, single-subject onset times were extracted based on Smulders (2010) and potential differences between signals were tested with conventional paired t-tests.

Finally, the time course of spatial selectivity was analyzed for both alpha-band responses and SSVEPs. First, the difference between the time courses of the attended and unattended stimuli was calculated for all conditions, respectively. Then, these difference time courses were subject to the identical analysis as described above to extract significant pre- to post-cue modulations and onset estimates of attentional spatial selectivity. Potential differences in the onset estimates of the spatial selectivity between signals were tested with conventional paired t-tests.

Task- and Attention-related Amplitude Changes of SSVEPs and Alpha-Band Oscillations

An additional analysis approach aimed at quantifying potential differences in amplitude values of alpha-band responses and

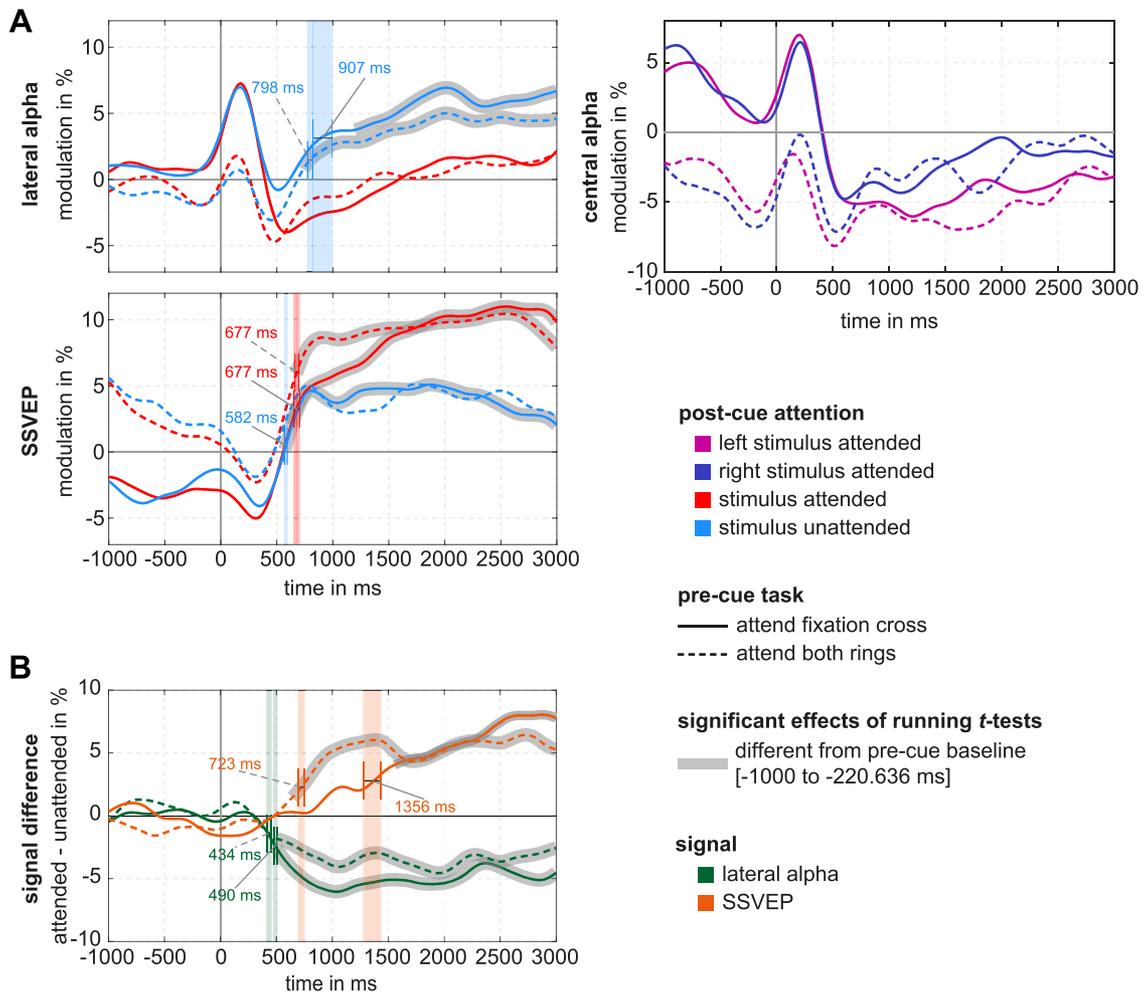


Figure 3. Amplitude time courses of SSVEP and alpha-band responses. (A) Gabor filtered time courses of signals, normalized to the grand mean pre-cue baseline (–1000 to –220.636 ms) averaged across all conditions, are shown for alpha-band responses contralateral to the stimulus (top left), SSVEPs (bottom left), and central alpha-band responses (top right), separately for all experimental conditions relative to cue onset (at 0 ms). Significant time points of running t-tests of the post-cue data points (500–3000 ms) that differed significantly from the pre-cue baseline of the respective signal and condition (–1000 to –220.636 ms) are shaded in gray. All results of the running t-tests were cluster corrected to control for false discovery rate (see Experimental Procedures). Onset times for which the pre- to post-cue modulation reached 50% were extracted via jackknifing procedure for each subject (see Experimental Procedures). Average onset times are marked, and the standard error of the subaverages, estimated according to (2010), is represented by horizontal error bars and shaded vertical bars. (B) Similarly, time courses, significant pre- to post-cue differences estimated with running t-tests and estimated onset ranges of these modulations, are plotted for the spatial attentional selectivity (i.e., difference curve for stimulus attended MINUS unattended) separately for both signals and both pre-cue tasks.

SSVEPs across task conditions for the entire pre- and post-cue time windows, respectively, and modeling their potential interaction. For this purpose, single-trial amplitude spectra were extracted with an untapered FFT for all experimental conditions: PRE-CUE TASK (attend fixation cross vs. attend both rings) and POST-CUE ATTENTION (attend left vs. attend right) separately for a pre-cue (–1000 to 0 ms) and a post-cue time window (500–3000 ms) for each channel and each subject. Again, the first 500 ms after the cue were discarded. Data were zero-padded to 16 384 points yielding a frequency resolution of 0.0156 Hz.

Additionally, in order to have similar spectral estimates for the longer post-cue time window as compared with the pre-cue time window, the post-cue amplitude spectrum was calculated by averaging FFT-amplitude spectra across four 1-s-long overlapping time windows (500–1500; 1000–2000; 1500–2500; and 2000–3000 ms). The same electrode clusters, derived from the grand mean topographies, were selected, as described above (see Fig. 2). Amplitude values of the left (14.167 Hz) and right (17 Hz)

SSVEP and left and right alpha oscillations (8–12 Hz) were then extracted separately for both time windows (pre- and post-cue), both pre-cue tasks (attend fixation cross and attend both rings) and both post-cue attention conditions (attend left and attend right).

Analogous to the procedure described for the Gabor-transformed data, for each subject, amplitude values were first normalized by the pre-cue amplitude averaged across all conditions. Signals from both left and right SSVEPs and alpha oscillations were then pooled by averaging across hemispheres to represent signal amplitudes contralateral to the attended and unattended stimulus independently of whether it was presented on the left or right side. Again, note that signals labeled as “contralateral to the unattended stimulus” are equivalent to signals “ipsilateral to the attended stimulus.” Overall, this yielded single-trial amplitudes of SSVEP and alpha responses contralateral to the stimuli, when either both or no stimulus was attended in the pre-cue time window (PRE-CUE TASK) and

when a ring was attended or unattended in the post-cue window (POST-CUE ATTENTION) separately for both time windows (TIME). Amplitude values for all signals were averaged across single trials of all factor combinations. For all signals (SSVEPs, lateral alpha responses, central alpha responses), potential differences between conditions were tested with a repeated-measures ANOVA (ANOVA_{RM}) with the within-subject factors POST-CUE ATTENTION and PRE-CUE TASK separately for both time windows.

In order to analyze signal modulations following the attentional shift, differences of pre- and post-cue amplitude values were first calculated for all signals. These difference values were then subject to an ANOVA_{RM} with the within-subject factors POST-CUE ATTENTION and PRE-CUE TASK. Potential pre-to-post cue changes in amplitude were then tested with post hoc t-tests against 0. This allowed us to disentangle whether attention-related changes were due to an amplitude modulation for the attended and/or unattended stimulus. Statistical analysis was performed in R (R Core Team 2016), using the package *afex* (Singmann et al. 2018) running in RStudio (RStudio Team 2016). Generalized Eta Squared (Bakeman 2005) and Cohen's D (Lakens 2013) served as estimates of effect sizes. For each signal, the results of ANOVAs and post hoc contrasts were corrected for multiple comparisons via the Bonferroni procedure.

Relation of Attentional Amplitude Modulation of SSVEPs and Alpha-Band Oscillations

In the next step, the potential relationship of alpha oscillations and SSVEP amplitudes was analyzed. It was specifically tested whether intraindividual differences in attention-related alpha-band modulations were related to differences in attention-related SSVEP amplitude modulations, i.e., do single-trial changes in alpha-band modulation explain some variance of single-trial SSVEP changes? In previous studies, contralateral decreases and ipsilateral increases in alpha-band amplitude (i.e., spatial attentional selectivity) were reported during spatial attentional shifts (Worden et al. 2000; Sauseng et al. 2005; Kelly et al. 2006; Thut et al. 2006; Rihs et al. 2007; Capotosto et al. 2009; Gould et al. 2011; Capilla et al. 2014; Frey et al. 2014; Ikkai et al. 2016; Feng et al. 2017; Foster et al. 2017; Green et al. 2017; Popov et al. 2017; Voytek et al. 2017; Heideman et al. 2018), and a graded lateralization of alpha-band amplitude was found to be related to graded behavioral effects of visuospatial attention (Thut et al. 2006). Here, we wanted to examine whether intraindividually graded alpha lateralization during spatial attention also relates to graded SSVEP amplitudes and hence indexes graded early sensory gain.

For this purpose, for each subject and each condition, the pre- to post-cue modulation of alpha-band lateralization was calculated for each trial (i.e., post-cue alpha amplitude modulations contralateral MINUS ipsilateral to the attended stimulus). Trials were then sorted according to this pre- to post-cue modulation of alpha-band lateralization, separately for the experimental conditions and each hemisphere (PRE-CUE TASK × POST-CUE ATTENTION × HEMISPHERE). The upper and lower 10% of trials (i.e., with highest and lowest values) were discarded to reduce the impact of potentially noisy trials. The remaining trials were binned into five overlapping bins equal in size and pooled across the left and right hemisphere to represent alpha-band and SSVEP amplitudes contralateral to the attended and unattended stimulus independently of whether it was presented at the left or right side. The first bin was comprised of trials

with pre- to post-cue amplitude modulations of alpha that were ipsilateral maximally larger than contralateral to the to-be-attended stimulus (i.e., maximizing the spatial selectivity and, thus, the representation of attended stimulus according to the assumed inhibitory role of alpha). Bin 5, on the other hand, contained trials with the opposite relationship (ipsilateral < contralateral; i.e., inverting the spatial attentional selectivity and, thus, maximizing the representation of the unattended stimulus according to the assumed inhibitory role of alpha). For these subsets of trials, pre-to-post attentional modulations of SSVEP amplitudes were then analyzed. Crucially, if attention-related alpha-band lateralization and early sensory gain control were related, due to the suggested inhibitory mechanism of alpha oscillations, SSVEP amplitudes should show the largest attention effect (attended > unattended) in the first bin and the smallest in bin 5 (see Fig. 5A for the conceptualization).

The impact of the strength of alpha lateralization on SSVEP amplitudes was tested with linear mixed models implemented in the package *lme4* (Bates et al. 2015) and *lmerTest* (Kuznetsova et al. 2017) implemented in R (R Core Team 2016). First, a maximally complex model was constructed, including the interactions between fixed factors PRE-CUE TASK (attend fixation cross vs. attend both rings), POST-CUE ATTENTION (attend left vs. right), and ALPHA BIN (bins 1–5) and intercept with random effects mirroring the fixed effect factors PRE-CUE TASK, POST-CUE ATTENTION, and ALPHA BIN grouped by the factor SUBJECT:

$$\text{SSVEP} \sim \text{POST-CUE ATTENTION} * \text{PRE-CUE TASK}$$

$$* \text{ALPHA BIN} + (\text{POST-CUE ATTENTION} * \text{PRE-CUE TASK}$$

$$* \text{ALPHA BIN} | \text{SUBJECTS}).$$

For the model selection, a backward elimination procedure was used, based on the function *lmerTest::step*. From the most complex hierarchically full model, effects are stepwise eliminated, and differences between the prediction of models were tested with an approximate F-test based on the Kenward–Roger's approach (Kenward and Roger 1997) reducing the model to contain only fixed factors and their interactions that significantly contribute to predicting SSVEP amplitudes. This allowed us to test whether the factor ALPHA BIN significantly contributed to explaining the variance of the SSVEP amplitude (i.e., whether SSVEP amplitude modulations were dependent on lateral alpha modulations).

Results

Behavioral Results

The behavioral task was designed to keep subjects engaged and vigilant. Participants detected on average 77.238% (SD = 9.003) of the targets in the post-cue task with a mean reaction time of 539.631 ms (SD = 40.047). In the pre-cue fixation task, they detected 95.833% (SD = 6.034) targets with a mean reaction time of 531.782 ms (SD = 70.279), and 84.583% (SD = 5.896) of pre-cue targets for the “both-rings” task were detected with a mean reaction time of 525.244 ms (SD = 45.610). The average false-alarm rate was 5.81% (SD = 3.21) for pre- and post-cue tasks in all trials.

Distinct and Separable Signals for SSVEPs and Alpha-Band Oscillations

As shown in Figure 2, our physical stimulation resulted in distinct SSVEP signals for both visual stimuli as revealed by

Table 1 ANOVA_{RM} table representing results of the analysis of FFT-derived amplitude values separately for all signals and time windows

Signal	Time	Factor	df	F-value	P-value	η_G^2
SSVEP	Pre	PRE-CUE TASK***	(1,19)	23.965	<0.001	0.463
		POST-CUE ATTENTION	(1,19)	1.327	0.7907	0.011
		POST-CUE ATTENTION × PRE-CUE TASK	(1,19)	0.564	1	0.005
	Post	PRE-CUE TASK	(1,19)	0	1	0
		POST-CUE ATTENTION**	(1,19)	16.651	0.0019	0.187
		POST-CUE ATTENTION × PRE-CUE TASK	(1,19)	0.44	1	0.002
	Post-pre	PRE-CUE TASK***	(1,19)	19.293	<0.001	0.132
		POST-CUE ATTENTION***	(1,19)	27.097	<0.001	0.211
		POST-CUE ATTENTION × PRE-CUE TASK	(1,19)	0.917	1	0.005
Lateral alpha-band responses	Pre	PRE-CUE TASK	(1,19)	3.847	0.1939	0.155
		POST-CUE ATTENTION	(1,19)	5.542	0.0884	0.012
		POST-CUE ATTENTION × PRE-CUE TASK	(1,19)	0.76	1	0.002
	Post	PRE-CUE TASK	(1,19)	0.538	1	0.003
		POST-CUE ATTENTION**	(1,19)	14.716	0.0033	0.166
		POST-CUE ATTENTION × PRE-CUE TASK	(1,19)	5.34	0.0967	0.005
	Post-pre	PRE-CUE TASK	(1,19)	1.145	0.8941	0.017
		POST-CUE ATTENTION***	(1,19)	20.27	<0.001	0.169
		POST-CUE ATTENTION × PRE-CUE TASK	(1,19)	1.454	0.7281	0.002
Central alpha-band responses	Pre	PRE-CUE TASK**	(1,19)	12.13	0.0075	0.301
		POST-CUE ATTENTION	(1,19)	0.495	1	0.005
		POST-CUE ATTENTION × PRE-CUE TASK	(1,19)	0.384	1	0.003
	Post	PRE-CUE TASK	(1,19)	0.328	1	0.001
		POST-CUE ATTENTION	(1,19)	5.706	0.0823	0.021
		POST-CUE ATTENTION × PRE-CUE TASK	(1,19)	0.477	1	0.001
	Post-pre	PRE-CUE TASK*	(1,19)	7.844	0.0342	0.098
		POST-CUE ATTENTION	(1,19)	4.049	0.1758	0.025
		POST-CUE ATTENTION × PRE-CUE TASK	(1,19)	0.922	1	0.002

Note: Main effects for the factors POST-CUE ATTENTION and PRE-CUE TASK are marked by asterisks and are written in italics with corresponding P-values written in bold.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

peaks in the grand mean FFT-spectrum. SSVEP signals showed a broad occipital topographical distribution with lateralized amplitude peaks. Additionally, we were able to independently analyze alpha oscillations in a frequency range of 8–12 Hz that also showed an occipital distribution with potentially two lateralized signal maxima and a central signal maximum.

Task- and Attention-Related Amplitude Modulation for SSVEPs and Alpha-Band Oscillations

The analysis of alpha-band and SSVEP amplitudes revealed the dynamics and topography of the task- and attention-related modulations for all signals during the pre- and post-cue periods, as well as specific pre- to post-cue modulations (see Figs 3 and 4).

SSVEP Amplitudes

As shown in Figure 3A (bottom left) and Figure 4A (bottom left) in the pre-cue period, SSVEPs were modulated by the pre-cue task. Specifically, SSVEP amplitudes elicited by both rings were higher when participants had to detect simultaneously presented targets in both rings compared with when they had to report changes in the fixation cross. This pattern was substantiated by the main effect PRE-CUE TASK for SSVEP responses ($P < 0.001$) for the whole pre-cue time period (see Table 1 and Fig. 4A).

In the post-cue period, following the shift of attention to any of the two stimuli, amplitudes were higher for the attended compared with the unattended stimulus as revealed by the main effect for the factor POST-CUE ATTENTION in the post-cue time window ($P = 0.002$) (see Fig. 4A, bottom middle column and Table 1).

Lastly, pre- to post-cue modulations were analyzed to examine the specific amplitude changes of SSVEP amplitudes for the attended and unattended stimulus following the attentional shift. SSVEP amplitudes were modulated differently depending on whether the stimulus became attended or unattended as revealed by the main effect of factor POST-CUE ATTENTION ($P < 0.001$) (see Table 1, and Fig. 4A, bottom right). This effect was present for both frequencies, particularly in occipital electrodes (see Fig. 4B). In addition, the size of the SSVEP amplitude modulation also depended on whether the fixation cross or both stimuli were attended in the pre-cue period (main effect of factor PRE-CUE TASK; $P < 0.001$); for both frequencies, this effect, again, was most prominent in occipital electrodes (see Fig. 4B). The exact pattern of pre- to post-cue modulations was disentangled with planned post hoc t-tests against 0. When participants attended to the fixation cross in the pre-cue time window, there was a significant post-cue increase for the SSVEP of the stimulus that became attended ($M = 11.970\%$; $SD = 9.90$; $t(19) = 5.404$; $P < 0.001$; $d = 1.239$), as well as the stimulus that became unattended, though smaller in amplitude ($M = 5.960\%$;

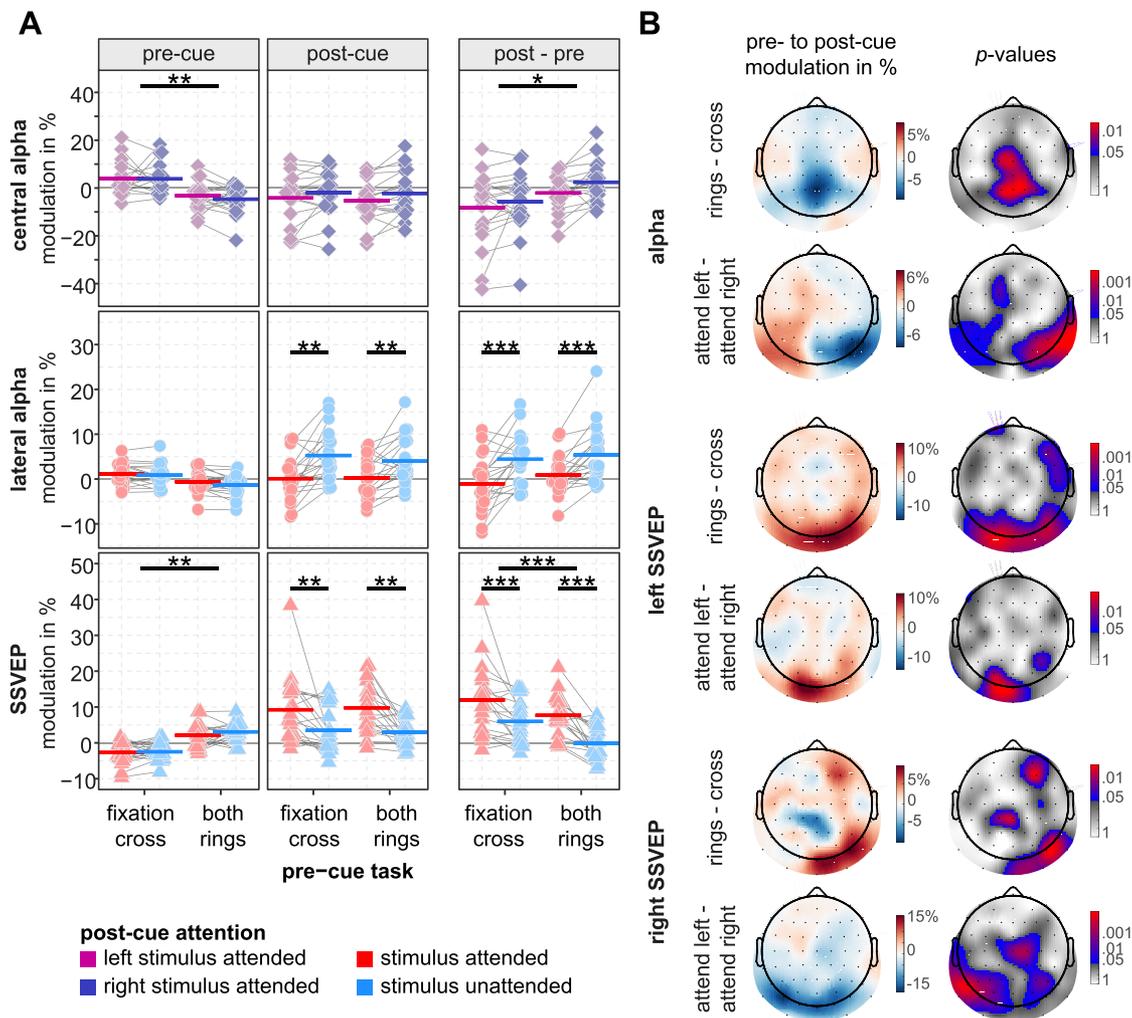


Figure 4. SSVEP amplitude and alpha-band responses and respective topographical distributions. (A) SSVEP amplitudes and alpha-band responses for all experimental conditions and time windows, respectively. Horizontal lines represent average FFT-derived amplitude modulations normalized to the grand-mean pre-cue baseline for each signal, separately for the pre-cue (−1000 to 0 ms) and the post-cue time window (500–3000 ms) and pre- to post-cue changes (post-cue–pre-cue). Single-subject data are represented by dots. For each signal, differences between amplitudes were tested with an ANOVA_{RM} for each time window (see Table 1). Main effects of factor POST-CUE ATTENTION and PRE-CUE TASK are marked by asterisks. *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$ (Bonferroni corrected). (B) Topographical distributions of the differences of the pre- to post-cue modulations contrasting the experimental conditions PRE-CUE TASK (rings vs. cross) and POST-CUE ATTENTION (attend left vs. attend right) for alpha-band oscillations (8–12 Hz) and left (14.167 Hz) and right (17 Hz) SSVEPs. The topographies of the related uncorrected P -values for each contrast are shown on the right side.

$SD = 5.98$; $t(19) = 4.461$; $P = 0.001$; $d = 1.023$). When participants already attended to both stimuli in the pre-cue task, the attentional shift after the cue led to an increase in amplitude for the attended ($M = 7.671\%$; $SD = 5.80$; $t(19) = 5.910$; $P < 0.001$; $d = 1.356$) but to no significant modulation of the unattended stimulus ($M = -0.157\%$; $SD = 4.47$; $t(19) = -0.157$; $P = 1$; $d = 0.036$).

Time course analysis via running t -tests revealed that SSVEP amplitudes were significantly increased relative to the pre-cue baseline from around 630 ms post-cue onwards to the end of the trial for the attended stimulus following both pre-cue tasks and also for the unattended stimulus after the fixation cross task (see Fig. 3A, bottom left). Jackknifing-based single-subject estimates of the time points for which the pre- to post-cue modulation reached 50% revealed an average latency of 677 ms ($SD = 494.61$) when subjects shifted attention from the fixation cross and 677 ms ($SD = 328.32$ ms) when they shifted their attention to one of the rings, after they needed to attend both rings in

the pre-cue task. As shown in Figure 3A, the average latency of the SSVEP amplitude increase for the “to-be-ignored” stimulus was 582 ms ($SD = 215.91$) when subjects shifted attention away from the fixation cross. Considering the time course of spatial selectivity, SSVEP amplitudes reached 50% of the post-cue amplitude after 1356 ms ($SD = 1497.29$) in the “attend fixation” and after 723 ms ($SD = 503.43$) in the “attend both rings” pre-cue task (Fig. 3B).

Alpha-Band Amplitudes for Lateral Electrodes

During the pre-cue period, amplitudes of lateral alpha responses were not significantly different when either both rings or the fixation cross were attended during the pre-cue period (no main effect of PRE-CUE TASK; see Table 1 and Fig. 4A, middle left).

In the post-cue period, following the shift of attention to any of the two stimuli, lateral alpha-band amplitudes were increased contralateral to the unattended as compared with the attended

stimulus, as revealed by the main effect for the factor POST-CUE ATTENTION ($P = 0.003$) in the post-cue time window (see Fig. 4A, middle column and middle row; Table 1).

For lateral alpha-band amplitudes, the analysis of pre- to post-cue modulations revealed that changes contralateral to the attended stimulus were significantly smaller than those contralateral to the unattended stimulus (i.e., ipsilateral to the attended stimulus) as shown by the significant main effect for the factor POST-CUE ATTENTION ($P < 0.001$), independent of the pre-cue task (no main effect for factor PRE-CUE TASK, see Table 1 and Fig. 4A, middle right). The lateralization of alpha-band amplitude due to the spatial attentional cue (attend left vs. right) was distributed across occipito-temporal electrodes (see Fig. 4B, second row). The effect was driven by a significant increase of alpha amplitude from pre- to post-cue, contralateral to the unattended stimulus independent of the pre-cue task, i.e., irrespective of attention being at the fixation cross in the pre-cue task ($M = 4.405\%$; $SD = 5.63$; $t(19) = 3.496$; $P = 0.010$; $d = 0.802$) or already at both rings ($M = 5.357\%$; $SD = 6.31$; $t(19) = 3.795$; $P = 0.005$; $d = 0.871$). For both pre-cue tasks, alpha contralateral to the attended stimulus was not significantly modulated from pre- to post-cue (pre-cue attend fixation cross: $M = -1.065\%$; $SD = 6.21$; $t(19) = -0.767$; $P = 1$; $d = 0.176$; pre-cue attend both rings: $M = 0.861\%$; $SD = 4.27$; $t(19) = 0.901$; $P = 1$; $d = 0.207$).

As shown in Figure 3A (top left), the analysis of the time courses via running t-tests revealed increases for alpha-band amplitudes contralateral to the unattended stimulus only. Jackknifing-based single-subject estimates of the time points for which the pre- to post-cue modulation reached 50% revealed an average latency of 907 ms ($SD = 1696.88$) for the signal contralateral to the unattended stimulus after the fixation cross task and 798 ms ($SD = 448.94$) after the “both rings” pre-cue task.

Although alpha-band responses were modulated on average 176 ms after SSVEP amplitudes, statistically this time difference was not significant, very likely due to the great variance within these measures (compare respective SDs). In numbers: direct comparison of modulation onsets following the “fixation cross” pre-cue task ($M = 230$ ms, $SD = 1780$ ms (SSVEP < lateral alpha); $t(19) = 0.578$, $P = 0.570$, $d = 0.129$), and ($M = 120$ ms, $SD = 602.43$ ms (SSVEP < lateral alpha); $t(19) = 0.896$; $P = 0.381$; $d = 0.200$) when subjects attended to both rings in the pre-cue period.

Spatial selectivity reached 50% of the post-cue amplitude after 490 ms ($SD = 247.92$) when attention was shifted from the fixation cross and after 434 ms ($SD = 354.23$) when both rings were attended in the pre-cue task (Fig. 3B). The direct comparison revealed this onset to be significantly earlier than that of spatial selectivity of the SSVEP modulations (pre-cue: attend fixation cross: $t(19) = 2.585$, $P = 0.018$, $d = 0.578$; pre-cue: attend both rings: $t(19) = 2.439$, $P = 0.025$, $d = 0.545$).

Alpha-Band Amplitudes for Central Electrodes

Central alpha-band responses were increased in amplitude when the fixation cross was attended compared with when both rings were attended during the pre-cue period. This pattern was substantiated by the main effect PRE-CUE-TASK for the whole pre-cue time period (see Table 1 and Fig. 4A, top left).

Following the attentional cue, central alpha-band amplitudes were similar and not significantly modulated by the factor POST-CUE ATTENTION (see Table 1 and Fig. 4A, top middle).

Pre-to-post modulations of central alpha-band amplitudes differed significantly depending on the PRE-CUE TASK, with larger decreases in amplitude when attention was previously at

the fixation cross compared with when it was deployed to both rings independently of the post-cue attention (no main effect for factor POST-CUE ATTENTION; see Table 1 and Fig. 4A, top right). This pre-cue task-dependent modulation of the alpha-band amplitude was distributed across centro-parietal electrodes (see Fig. 4B, first row). Planned comparisons revealed that the overall central alpha-band amplitude was not significantly different from the pre-cue baseline in any of the experimental conditions: pre-cue attend fixation cross, post-cue attend left ($M = -8.21\%$; $SD = 14.98$; $t(19) = -2.45$; $P = 0.097$; $d = 0.562$), pre-cue attend fixation cross, post-cue attend right ($M = -5.78\%$; $SD = 12.24$; $t(19) = -2.11$; $P = 0.192$; $d = 0.485$), pre-cue attend both rings, post-cue attend left ($M = -2.09\%$; $SD = 7.52$; $t(19) = -1.24$; $P = 0.918$; $d = 0.285$), and pre-cue attend both rings, post-cue attend right ($M = -2.44\%$; $SD = 8.19$; $t(19) = 1.33$; $P = 0.800$; $d = 0.305$).

No Relation of Attentional SSVEP and Alpha-Band Amplitude Fluctuations

In the next step, we examined whether within-subject fluctuations in the lateralization of visual alpha-band amplitudes (i.e., fluctuations in spatial attentional selectivity) are systematically related to changes in SSVEP amplitudes. Do trials with strong changes in alpha-band lateralization (alpha contralateral to the unattended stimulus minus contralateral to attended stimulus) also show the strongest attentional modulation of SSVEP amplitude (see Fig. 5A)? A comparison between different linear mixed effect models revealed that models including the factor ALPHA-BIN (or any interaction with any other factor) did not systematically differ from models without this factor ($P_s > 0.221$), while models without the factor POST-CUE ATTENTION ($P < 0.001$) and PRE-CUE TASK ($P < 0.001$) differed significantly from models not including them (see Table 2). The factor ALPHA-BIN did not significantly explain additional variance and the model that fitted the data best is:

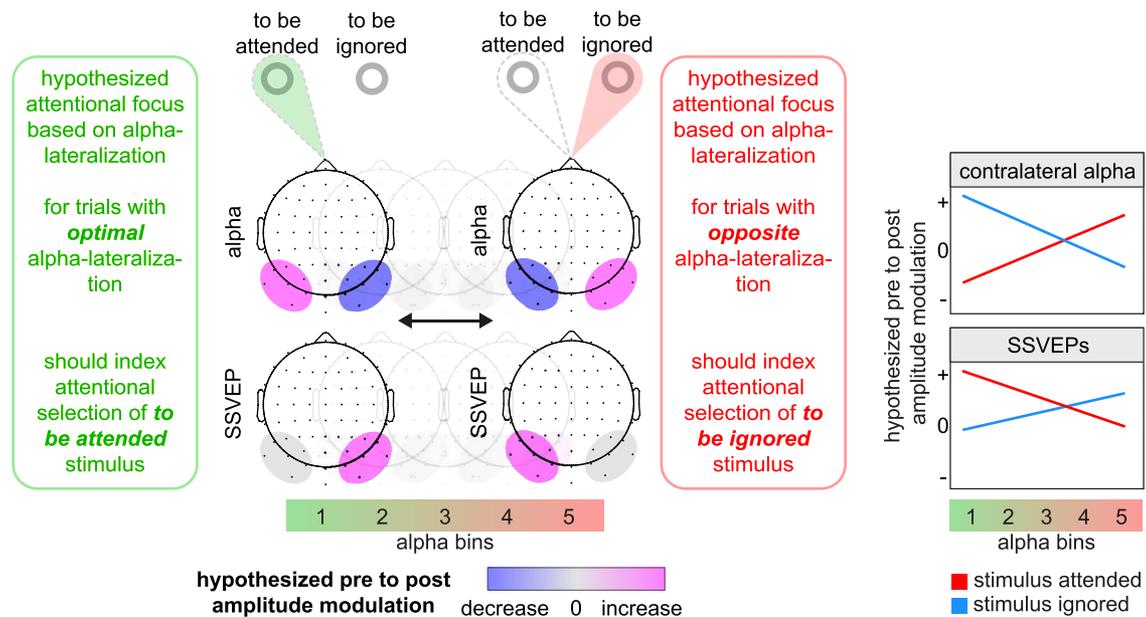
$$\begin{aligned} \text{SSVEP} &\sim \text{POST-CUE ATTENTION} + \text{PRE-CUE TASK} \\ &+ (\text{POST-CUE ATTENTION} * \text{PRE-CUE TASK} \\ &* \text{ALPHA BIN} \mid \text{SUBJECTS}). \end{aligned}$$

This analysis mirrored the ANOVA results for SSVEP amplitudes presented above and substantiated that attention-related amplitude modulations of SSVEPs are independent of a graded alpha-band lateralization, as shown in Figure 5B; while attentional alpha-band modulations clearly differ between different alpha bins, this is not the case for SSVEP amplitude modulations and contrary to the hypotheses derived from a model posing a relationship between alpha-band- and SSVEP-modulations (see Fig. 5A). Additionally, these results were mirrored when only absolute fluctuations of the post-cue alpha lateralization independent of pre-cue baseline fluctuations were taken into account (see Supplemental Results).

Discussion

The main objective of this study was to assess if alpha-band modulations represent a neural mechanism of visual spatial attention that “directly” influences early sensory gain during sustained stimulus processing. To this end, we recorded EEG activity in a spatial cueing paradigm, in which we presented flickering stimuli in the left and right visual hemifield to

A hypothesized relationship between SSVEP and alpha amplitude modulation for different alpha bins



B found modulation of SSVEP and alpha amplitude for different alpha bins

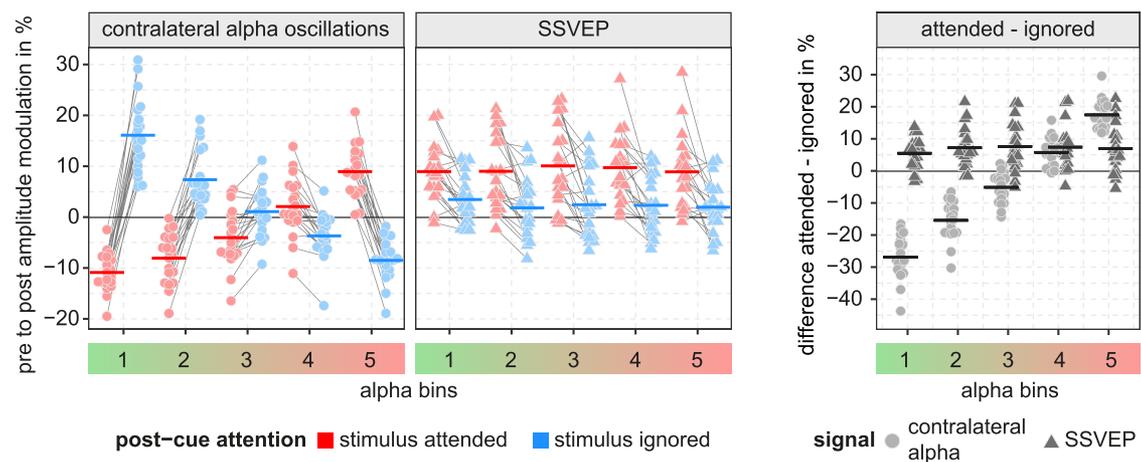


Figure 5. Amplitude modulations of lateral alpha-band amplitudes and SSVEPs for separate alpha bins, respectively. (A) Trials were sorted according to their pre-to-post lateralization (i.e., spatial attentional selectivity) of alpha-band amplitudes. Bin 1 was comprised of trials for which alpha-band amplitude modulations were maximally larger ipsilateral than contralateral to the to-be-attended stimulus (i.e., maximizing the spatial selectivity and thus the cortical representation of the attended stimulus according to the assumed inhibitory role of alpha). Bin 5, on the other hand, contained trials with the opposite relationship (ipsilateral < contralateral to the attended stimulus; i.e., inverting the spatial attentional selectivity and thus maximizing representation of the unattended stimulus). In line with the inhibitory role of alpha-band oscillations, increases of SSVEP amplitude for the attended stimulus should be expected for bin 1, while increases for the unattended stimulus should be expected for bin 5. Hypothesized amplitude modulations of SSVEP and contralateral alpha-band amplitudes are shown on the right side. (B) For the subsets of trials within each alpha bin, pre-to-post amplitude modulations are plotted for contralateral alpha-band and SSVEP amplitudes separately when the stimulus was attended or unattended (left and middle figure). The difference of attended-ignored is plotted on the right side. For lateral alpha-band amplitudes, the amplitude values depend on the alpha bin, as well as the post-cue attention. For SSVEPs, however, amplitude modulations do not differ systematically between alpha bins and solely depend on the post-cue attention condition and are always larger for the attended as compared with the unattended stimulus.

assess the dynamics of alpha-band responses and early sensory processing as a function of spatial attention. Importantly, we controlled for spatial visual attention “before” the shifting cue instructed participants to shift attention to the left or right visual hemifield.

We replicated the findings of significantly increased alpha-band activity for the to-be-ignored compared with the to-be-

attended location at the respective lateral posterior electrodes. This pattern is commonly reasoned as electrophysiological evidence for the role of alpha-band oscillations as a mechanism for top-down modulated “active” suppression of task-irrelevant or to-be-ignored information (Worden et al. 2000; Sauseng et al. 2005; Kelly et al. 2006; Thut et al. 2006; Rihs et al. 2007; Capotosto et al. 2009; Gould et al. 2011; Payne et al. 2013; Capilla et al.

Table 2 Results of backward elimination procedure for modeling the relationship between POST-CUE ATTENTION condition PRE-CUE TASK and ALPHA BIN representing alpha lateralization

Factor	Eliminated	df	F-value	P-value
POST-CUE ATTENTION × PRE-CUE TASK × ALPHA BIN	Yes	(1,19)	1.6	0.2212
POST-CUE ATTENTION × ALPHA BIN	Yes	(1,19)	0.215	0.6484
PRE-CUE TASK × ALPHA BIN	Yes	(1,19)	0.447	0.5119
POST-CUE ATTENTION × PRE-CUE TASK	Yes	(1,19)	0.046	0.8317
ALPHA BIN	Yes	(1,19)	0.511	0.4835
POST-CUE ATTENTION***	No	(1,19)	30.529	<0.001
PRE-CUE TASK***	No	(1,19)	22.279	<0.001

Note: The hierarchical full model is step-by-step compared with a less complex model for which single factors or their interactions are eliminated. Factors, which can be eliminated, i.e., for which the less complex model does not significantly differ from the complex model are marked by "yes" in the column "eliminated," and corresponding F- and P-values are shown. Degrees of freedom are estimated via Kenward-Roger's approach (Kenward and Roger 1997). Significant factors are marked and are written in italics with corresponding P-values written in bold. *** $P < 0.001$.

2014; Frey et al. 2014; Ikkai et al. 2016; Feng et al. 2017; Foster et al. 2017; Green et al. 2017; Popov et al. 2017; Voytek et al. 2017; Heideman et al. 2018). Crucially, the processing level at which this hypothesized suppressive mechanism may be instantiated is still unrefined. Whereas early work (Foxe and Snyder 2011) assumes alpha to be effective for modulating early sensory processing (i.e., early sensory gain control), more recent work proposes alpha to be relevant for a modulation of later perceptual processing levels (Chaumon and Busch 2014; Limbach and Corballis 2016; Benwell et al. 2017; Iemi et al. 2017; Samaha et al. 2017; Iemi and Busch 2018). However, a drawback of these studies was that they did not directly test the relation between alpha and early sensory gain control in the human brain.

Contrary, the present study was designed to directly address this issue. Our results clearly show that attentional SSVEP amplitude modulations and alpha-band oscillations measured by their amplitude vary independently from each other and exhibit dynamics that do not support the notion that alpha-band modulation is a neural control mechanism of early sensory gain.

First, attentional modulations of both signals in relation to the pre-cue baseline did not match the pattern proposed by an inhibitory account of alpha-band oscillations; while SSVEP amplitudes increased with attention, alpha-band responses, in contrast, were not modulated contralateral to the attended stimulus, speaking against the idea that a decrease in alpha reflects the facilitation of the to-be-attended stimuli (cf. Klimesch et al. 2007; Romei et al. 2008b; Romei et al. 2008a; Jensen and Mazaheri 2010). Additionally, alpha-band amplitude increases contralateral to the unattended stimulus were not mirrored by decreases in SSVEP amplitude at the corresponding electrode sites. On the contrary, relative to the pre-cue level when the fixation cross was attended, the SSVEP and alpha-band amplitudes increased together for the to-be-ignored side (compare solid blue lines in Fig. 3A).

Second, SSVEP amplitudes captured pre-cue attentional demands, as they were already higher when both lateral stimuli were attended before cue onset. Thus, SSVEP response patterns reliably captured differences in stimulus processing due to attention and task demands. Critically, lateral alpha-band responses only captured post-cue attention dynamics, as they were increased contralateral to the unattended stimulus but did not reliably differ when both stimuli were either attended or unattended during the pre-cue period.

Third, the temporal dynamics of the attentional modulation relative to the pre-cue baseline do not suggest that alpha-band

modulations have a leading role for (i.e., precede) SSVEP modulations. Interestingly, the time courses of spatial selectivity revealed an earlier onset of alpha-band amplitude modulations compared with SSVEPs.

Fourth, and most strikingly, trial-by-trial attentional dynamics of SSVEP amplitudes (i.e., spatial selectivity) were independent of trial-by-trial dynamics of alpha-band lateralization. Critically, attention-related SSVEP amplitude modulations were indistinguishable between subgroups of trials with a graded alpha-band lateralization, i.e., a graded spatial attentional selectivity.

Taken together, our findings strongly argue against the role of alpha-band oscillations as a top-down neural mechanism that modulates early sensory gain for attended or unattended stimuli and suggests that alpha-band modulations and early sensory gain (i.e., facilitation and/or suppression) seem to index two unrelated neural mechanisms of spatial attention with different temporal dynamics.

Nevertheless, our results need to be discussed in the light of a vast amount of studies that found modulations of alpha-band responses during tasks involving spatial attention in the visual (Worden et al. 2000; Sauseng et al. 2005; Kelly et al. 2006; Thut et al. 2006; Rihs et al. 2007; Capotosto et al. 2009; Gould et al. 2011; Capilla et al. 2014; Frey et al. 2014; Ikkai et al. 2016; Feng et al. 2017; Foster et al. 2017; Green et al. 2017; Popov et al. 2017; Voytek et al. 2017; Heideman et al. 2018), somatosensory (Jones et al. 2010; Haegens et al. 2011, 2012; Forschack et al. 2017), or auditory domain (Hartmann et al. 2012; Wöstmann et al. 2016, 2017). In line with the present results, these studies found higher alpha-band responses contralateral to the unattended as compared with the attended stimulus and reasoned a functional role of this modulation. Some mixed findings exist whether alpha-band differences are due to an increase in amplitude ipsilateral (Worden et al. 2000; Kelly et al. 2006; Rihs et al. 2007, 2009) or due to a decrease contralateral to the attentional focus (Sauseng et al. 2005; Thut et al. 2006; Ikkai et al. 2016). However, besides these differences, the general notion is that the lateralization or spatial selectivity of alpha-band oscillations represents an active mechanism associated with the attentional modulation of behaviorally relevant information.

Importantly, in many previous studies, temporal dynamics of alpha-band responses were not assessed during concurrent visual stimulation and attentional manipulation thereof. Rather, prestimulus alpha levels or alpha levels in a time interval between a cue and the upcoming stimulus have been analyzed.

On the one hand, this could have confounded spatial attentional selection with expectancy effects and—on the other hand—did not allow for a concurrent analysis of neural activity in early visual cortex and alpha-band responses, rendering any proposed relation between alpha-band oscillations and its mechanistic role for early sensory gain control rather speculative. Additionally, the reported prestimulus alpha-band levels may represent and may be driven by additional variations of arousal, idling, or vigilance that may rely on different neural mechanisms and may be different from a top-down “active” inhibition or suppression of incoming sensory information. Future studies will need to disentangle the different contributions of dynamics in factors such as vigilance, arousal, attention and task demands on alpha-band dynamics, and their relation to or consequence on behavior and perception.

In a recent study, Keitel et al. (2019) examined modulations of SSVEPs for either attended or unattended stimuli that flickered in the alpha-band range. By analyzing their data with two conventional analysis regimes, emphasizing either evoked or induced activity in the signals, they elegantly showed a reverse of the attentional amplitude modulation when contrasting signals contralateral to the attended and unattended stimulus. Evoked SSVEP signals were increased for the attended versus unattended stimulus, whereas the opposite pattern was found for induced alpha-band activity, although both signals indeed overlapped in the frequency space. A missing co-modulation of both signals supported the independence of SSVEP signals and alpha-band amplitudes. These findings are well in line with ours, and the current data complement their findings by an unbiased estimation of the attentional modulation of alpha-band oscillations and SSVEPs (there is no overlap in frequency space in our study) with an experimentally controlled baseline. Therefore, the present study goes beyond existing studies by concurrently analyzing and assessing visuospatial attentional dynamics of independent alpha-band modulations and sustained sensory representations.

If neural dynamics in the alpha-band do not represent an attentional mechanism altering the early sensory representation of stimuli, what might be the functional relevance of alpha oscillations? Historically, alpha-band oscillations have been conceptualized as an “idling rhythm,” indexing a resting-state activity in the brain that increases during the phases of reduced or absent stimulus processing (Pfurtscheller et al. 1996). Alpha-band oscillations could thus represent an epiphenomenon of changes in stimulus processing due to hidden attentional dynamics. However, if alpha-band oscillations were not seen as a mechanism of attention but as a marker of neural processing in general, their fluctuations should still index attention-related fluctuations in neural processing. Attention-related fluctuations in alpha-band amplitude should thus still correspond to fluctuations in SSVEP amplitude. This, however, was not the case in the present study.

Alpha-band modulations have been shown to be reliably associated with behavior: increased alpha-band amplitudes in task-relevant areas seem to be associated with degraded performance, again reasoned as a consequence of inhibition (Thut et al. 2006; Capotosto et al. 2009; Gould et al. 2011; Capilla et al. 2014; Feng et al. 2017; Foster et al. 2017; Popov et al. 2017; Voytek et al. 2017). These correlational findings are extended by experiments using brain stimulation techniques such as transcranial magnetic stimulation or transcranial alternating stimulation to directly modulate alpha-band oscillations. These experiments studied the behavioral consequences of external stimulation in

various tasks, such as the detection of near-threshold stimuli. In these studies, modulations in performance (e.g., increase of detection threshold) were found to be linked to changes in alpha-band amplitude (Romei et al. 2010, 2012; Müller et al. 2015; Wöstmann et al. 2018; Craddock et al. 2019) and phase (Neuling et al. 2012; Cecere et al. 2015; Gundlach et al. 2016; Helfrich et al. 2017) pointing towards the inhibitory role of alpha-band oscillations. These findings specifically argue against a pure idling role of alpha-band oscillations and suggest a functional relevance of alpha. Nevertheless, none of these studies revealed a relation between alpha-band modulations and sensory gain control but rather between alpha-band modulations and changes in behavior. Thus, it is possible that alpha-band modulations exert their influence at a later stage in the processing cascade beyond early neural stimulus representation. In this line, studies implanting graph-theoretical approaches have shown that differences in alpha-band amplitudes could be linked to differences in whole-brain information transfer in auditory and somatosensory networks as measured with MEG (Weisz et al. 2014; Leske et al. 2015) and within visual networks as measured with fMRI (Scheeringa et al. 2012; Mo et al. 2013; Zumer et al. 2014). Furthermore, increases in alpha-band amplitude during a visual search paradigm in rhesus monkeys did not arise for mere distracting search regions but specifically for behaviorally irrelevant search regions that have previously been fixated (Mirpour and Bisley 2013), supporting the idea that alpha-band oscillations are related to the behavioral consequences of certain stimuli. Interestingly, preparatory alpha-band modulations in a spatial cueing design were rather associated with a modulation of the late response-relevant P3b component, whereas a different preparatory slow wave potential indexed differences in the early N1 component (Grent-t-Jong et al. 2011).

In a recent study, implementing a visual detection task, penalizing either misses or false alarms led to the modulation of alpha-band amplitude that in turn increased the output activity of the visual cortex in the gamma range and thereby directly shifted the decision bias (Kloosterman et al. 2019). This again suggests a more prominent role of alpha-band oscillations in response selection processes relevant for behavior. Furthermore, there is accumulating evidence from studies examining spontaneous fluctuations of alpha-band amplitude outside a strict attentional experimental framework. These studies reported that there is indeed no relationship between decreases in alpha-band amplitudes and increases in sensory precision and/or behavioral accuracy. Instead spontaneous alpha-band fluctuations could be linked to a modulation of the tendency to respond per se (i.e., response to targets “and” distractors; the response criterion) but could not be linked to a modulation of sensitivity (i.e., the selective increase of responses to target stimuli) in visual (Limbach and Corballis 2016; Iemi et al. 2017) or somatosensory (Craddock et al. 2017) detection and discrimination tasks. Irrespective of the actual accuracy, spontaneous alpha-band fluctuations were also predictive of the confidence of the decision in a visual discrimination task (Samaha et al. 2017) or awareness of experience in visual (Benwell et al. 2017; Iemi and Busch 2018) or auditory (Wöstmann et al. 2019) discrimination tasks. Mapping the response functions in a visual detection task for stimuli of varying contrasts separately for different levels of fluctuating visual alpha-band amplitude, Chaumon and Busch (2014) found evidence for a relationship between alpha and behavior that is supportive of a response gain rather than a contrast gain function, again stressing the role of alpha-band

oscillations at a postperceptual level beyond early sensory processing. However, whereas these studies assume sensory representation to be unaffected by alpha-band fluctuations, they have never directly tested that assumption. Hereby, our study very well complements these findings by showing that alpha-band oscillations in the context of a top-down spatial attention task are actually unrelated to the early sensory gain control altering neural processing of to-be-attended and unattended stimuli.

Surprisingly, spatial selectivity of alpha-band oscillations seems to develop earlier than that of SSVEPs, which is in stark contrast to the notion that alpha modulations may represent postperceptual relevant processes. One speculative explanation may be based on findings that for stimuli presented in both visual hemifields, processing resources may (partly) be attributed independently (Alvarez and Cavanagh 2005; Delvenne and Holt 2012; Walter et al. 2013; Störmer et al. 2014). Accordingly, the attentional selection of one of the two stimuli may lead to the facilitation of the attended stimulus as reported in the current study, but not necessarily to a reduction in amplitude for the unattended stimulus of the other hemifield (see also: Müller 2008; Kashiwase et al. 2012). The SSVEP time course of the difference between the attended and unattended stimulus may thus be largely driven by the sensory gain for the spatially attended stimulus. Alpha-band modulations on the contrary were shown to be associated with increases contralateral to the unattended (Worden et al. 2000; Kelly et al. 2006; Rihs et al. 2007, 2009) as well as decreases contralateral to the attended stimulus side (Sauseng et al. 2005; Thut et al. 2006; Ikkai et al. 2016). As alpha modulations seem to affect both hemispheres diametrically, the calculation of the difference may increase the representation of the modulation and allow for a more robust estimation of the onset. This is substantiated by the fact that the variance of the estimated onset times for alpha-band oscillations is lower than that of the SSVEPs and that of the alpha-band pre- to post-cue amplitude modulations. Besides this, a modulation pattern spread across both hemispheres may again point towards the relevance of alpha-band oscillations upon the modulation of a postperceptual and integrative processing level.

Another potential explanation for the lack of a relationship between alpha-band responses and SSVEPs could be that attentional modulations of alpha-band responses are related to different attentional mechanisms than those affecting SSVEP modulations. While attentional SSVEP modulations have been mostly linked to changes in sensory gain (Di Russo et al. 2001; Kim et al. 2007; Müller and Hillyard 2000) and changes in neural synchrony (Norcia et al. 2015), alpha-band modulations could potentially be related to different aspects of attention: such as noise reduction or an alteration of sensory normalization (Carrasco 2011; Maunsell 2015; Kastner and Buschman 2017). Thereby, alpha-band activity may exert its influence on early sensory processing not reflected by the SSVEP responses. Future studies should elucidate this possibility by using different neural measures of early sensory processing.

In the present experimental task, attention-related alpha-band dynamics related to the pre- versus the post-cue task seem to be mapped differently. While lateral occipital alpha-band responses were modulated by post-cue attentional demands and lateralized depending on the spatial attentional focus, alpha-band responses measured more centrally were rather modulated by differences during the pre-cue task. It is surprising that lateral alpha-band responses, which indeed track

differences between attending to one or the other lateralized stimulus, do not differ when stimuli were attended either bilateral or not at all. This may implicate that different alpha-band generators may be associated with different aspects of the task, as suggested by Sokuliuk et al. (2019). These authors reported a centro-parietal alpha-band component that was modulated rather by task effort than by attentional focus. Besides differences in the spatial attentional focus, alpha-band amplitude changes in the central cluster may also arise from differences in task demands between both pre-cue tasks (detect changes in both rings vs. changes at fixation cross) and potential differences in the task difficulty as revealed by the behavioral results. Nonetheless, pre-cue differences of task difficulty and task demands seem not to confound the post-cue attentional allocation of attention. In this line, our analyses of SSVEPs and alpha-band oscillations did not show any interaction between the post-cue attentional modulation and the pre-cue related changes in amplitude. As the distribution of SCDs does not necessarily reveal the underlying neural generators (Tenke and Kayser 2012; Kayser and Tenke 2015), the exact anatomical localization of underlying generators of these amplitude modulations by attentional and task demands will have to be subject to future studies.

Taken together, the present results clearly disqualify the idea that the modulation of alpha-band oscillations is a neural mechanism that directly alters early sensory gain for continuously presented stimuli under sustained spatial attentional selection. Attentional task requirements modulated the amplitude of alpha responses and SSVEP amplitudes independently. In addition, alpha-band amplitude modulation did not lead the modulation of SSVEP amplitudes. Attentional dynamics of early sensory gain control and alpha-band oscillations may thus represent different components or features of visuospatial attention. This is well in line with the notion that attention represents an aggregate process, which spans different attentional mechanisms at distinct processing levels, serving to affirm a meaningful interaction with the environment (Buschman 2015; Luo and Maunsell 2015; Maunsell 2015). Future studies will have to elucidate the potential functional role of alpha-band oscillations beyond altering early sensory processing.

Supplementary Material

Supplementary material is available at *Cerebral Cortex* online.

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Author Contributions

C.G. and M.M.M. designed the study. C.G. and N.F. analyzed data. S.M. contributed to data analysis. C.G., S.M., N.F., M.M.M. wrote the manuscript.

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