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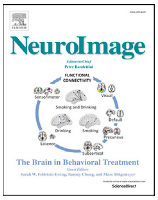

Too little, too late, and in the wrong place: Alpha band activity does not reflect an active mechanism of selective attention

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A R T I C L E I N F O

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A B S T R A C T

Selective attention focuses visual processing on relevant stimuli in order to allow for adaptive behaviour despite an abundance of distracting information. It has been proposed that increases in alpha band (8–12 Hz) amplitude reflect an active mechanism for distractor suppression. If this were the case, increases in alpha band amplitude should be succeeded by a decrease in distractor processing. Surprisingly, this connection has not been tested directly; specifically, studies that have investigated changes in alpha band after attention-directing cues have not directly assessed the neuronal processing of distractors. We concurrently recorded alpha activity and steady-state visual evoked potentials (SSVEPs) to assess the processing of target and distractor stimuli. In two experiments, participants covertly shifted attention to one of two letter streams (left or right) to detect infrequent target letters 'X' while ignoring the other stream. In line with previous findings, alpha band amplitudes contralateral to the unattended location increased compared to a pre-cue baseline. However, there was no suppression of SSVEP amplitudes elicited by unattended stimuli, while there was a pronounced enhancement of SSVEPs elicited by attended stimuli. Furthermore, and crucially, changes in alpha band amplitude during attention shifts did not precede those in SSVEPs and hit rates in both experiments, indicating that changes in alpha band amplitudes are likely to be a consequence of attention shifts rather than the other way around. We conclude that these findings contradict the notion that alpha band activity reflects mechanisms that have a causal role in the allocation of selective attention.

1. Introduction

Visual selective attention enhances the processing of behaviourally relevant stimuli (Posner, 1980) through a sensory gain mechanism, which magnifies the neuronal responses to attended stimuli compared to unattended stimuli without qualitatively changing them. For example, firing rates increase without changes to the width of tuning curves (Treue and Martinez-Trujillo, 1999) and scalp-recorded potentials are enhanced without changes in their topographical distribution (Hillyard et al., 1998). Whether such attentional modulations mainly reflect suppressive or facilitatory mechanisms is still a matter of debate, and so is the question about how they are enacted.

Alpha oscillations (8–12 Hz), which were traditionally considered to reflect idling (reviewed in Pfurtscheller et al., 1996), have more recently been proposed as an inhibitory attentional mechanism. This *alpha suppression hypothesis* was initially advanced by Kelly et al. (2006), who found that alpha amplitudes were enhanced contralateral to an ignored location, which they interpreted as a signature of active suppression of distracting input. Consistent with this view, other studies have sought to link lateralized changes in alpha amplitude with spatial attention and argued that alpha mediates the observed attentional effects (Sauseng et al., 2005; Thut et al., 2006; Bacigalupo and Luck, 2019). Higher alpha amplitudes have also been found to correlate with higher thresholds for detecting and discriminating a variety of stimuli (Ergenoglu et al., 2004; van Dijk et al., 2008; Mathewson et al., 2009; Wyart and Tallon-Baudry, 2009), and have been observed in preparation for upcoming visual distractors (Worden et al., 2000). Alpha-enhancement was observed to be location specific to unattended areas even when eight different locations were tested (Rihs et al., 2007). These findings have been taken to suggest that, rather than idling, alpha-enhancement reflects an active retinotopically organised mechanism for suppressing distractors.

Other potential functional roles of alpha oscillations have also been suggested (see discussion and review by Van Diepen et al., 2019). For example, the 'pulsed-inhibition hypothesis' posits that alpha influences perception in a phasic manner (Jensen et al., 2012), while others have suggested that alpha is related to post-perceptual processing stages,

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rather than direct sensory modulation (Chaumon and Busch, 2014; Limbach and Corballis, 2016). Here, we specifically focus on the prominent alpha-suppression hypothesis (Kelly et al., 2006; Jensen and Mazaheri, 2010), which suggests that alpha amplitude reflects a mechanism that directly causes distractor suppression.

However, a recent study found that preparatory alpha amplitude did not mediate suppression for known distractor locations when target locations remained uncertain (Noonan et al., 2016), casting doubt on the suggestion that alpha amplitude reflects suppression. Further, the evidence that has been garnered to support the alpha suppression hypothesis appears not to be as compelling as previously thought (Keitel et al., 2019; Foster and Awh, 2019; Gundlach et al., 2020). If increased alpha amplitude reflects a causal mechanism for attentional suppression, then increased alpha amplitude should precede distractor suppression at the corresponding retinotopic location. However, earlier studies have not tested the link between the time course of alpha activity and distractor processing. For example, Kelly et al. (2006), while measuring alpha amplitudes, did not report any neuronal measure of distractor processing. Hence, it would be premature to conclude that alpha suppresses distractors. Furthermore, studies that investigated the time-course of attentional modulation of stimulus processing after attention-directing cues reported enhanced processing of attended stimuli, but no suppression of unattended stimuli (Müller et al., 1998; Müller and Hillyard, 2000; Kashiwase et al., 2012). However, none of these studies analysed alpha activity. Finally, it is not clear if alpha increases precede or follow attentional shifts since alpha amplitude increases typically start and peak much later than estimates of attentional shift times (Müller and Rabbitt, 1989; Carlson et al., 2007; Horowitz et al., 2009; Chakravarthi and VanRullen, 2011). Hence, the link between alpha and distractor suppression seems indirect at best.

Here we directly test this link by modifying the paradigm used by Kelly et al. (2006) to concurrently measure alpha amplitudes and neural processing of attended and unattended stimuli during cued shifts of spatial attention in two experiments through recordings of steady-state visual evoked potentials (SSVEPs). SSVEPs are oscillatory brain responses with the same frequency as the flickering stimulus driving them. Their amplitude is modulated by selective attention (Morgan et al., 1996), allowing one to concurrently measure the allocation of attention in a multi-stimulus display by flickering each stimulus at a separate frequency ('frequency-tagging'). If alpha amplitude enhancement reflects an active mechanism for distractor suppression, then increases of alpha amplitude should cause a subsequent suppression of SSVEP amplitudes elicited by unattended distractors.

2. Method

2.1. Experiment 1

2.1.1. Participants

Nineteen participants (self-reported: 7 males, 2 left-handed, aged: 19–42 years, median age = 23) volunteered in Experiment 1. Three were excluded from all analyses as they had less than 35% trials remaining in at least one condition after artefact rejection of their EEG data (eye movements, blinks, etc.), leaving a sample size of sixteen. Participants provided written informed consent, reported normal or corrected-to-normal vision, and were reimbursed (£10) for their time. The experiment was approved by the Psychology Ethics Committee at the University of Aberdeen.

2.1.2. Stimuli and procedure

Stimuli were presented on a 20-inch CRT monitor with a resolution of 640 × 480 pixels, refresh rate of 120 Hz, and viewed at a distance of ∼60 cm. Stimulus generation and response collection were controlled through Matlab (The MathWorks, Natick, MA) using Cogent Graphics (John Romaya, Laboratory of Neurobiology at the Wellcome Department of Imaging Neuroscience).

Our paradigm was adapted from Kelly et al. (2006)'s study to allow for precise assessment of the time-course of behavioural performance, SSVEP amplitudes, and alpha band amplitudes. Participants were asked to rapidly indicate the presence of infrequent target letters 'X' embedded in a letter stream on the cued side by pressing the space bar, while ignoring 'X's in a letter stream on the opposite side. Each trial lasted 14 s and started with a 5 s rest period (indicated to participants by a green fixation cross; CIE 1976: $u^* = 0.12$, $v^* = 0.56$, $L^* = 42.3$) which turned red (CIE 1976: $u^* = 0.43$, $v^* = 0.52$, $L^* = 12.5$) for 0.5 s to warn participants of the upcoming stereo auditory cue (0.5 s; played from two speakers to the left and right of the monitor). The cue indicated the to-be attended side by saying "Left" or "Right". The fixation cross turned white with the onset of the auditory cue and participants performed the detection task for 8.5 s, after which the fixation cross changed back to green to signify the beginning of the next rest period. Participants were instructed to blink and not to respond to 'X's during the rest period. The fixation cross and the two letter streams thus stayed on screen continuously throughout each block of trials.

Two streams of black letters were presented on white squares (4.7 × 4.7° of visual angle; luminance = 59.6 cd/m^2) centred 5.5° to the left and right of a central fixation cross (width and height 0.65°) on an otherwise dark background (Fig. 1). The letter streams consisted of a random sequence of uppercase letters from 'A' to 'H' ('Arial', font size: 35, ∼1.2° in height) without consecutive repetitions. The white squares flickered (left square: 15 Hz; right square: 20 Hz) in order to elicit steady-state visual evoked potentials (SSVEPs) and the letters changed synchronously on both sides at a rate of 4 Hz, also eliciting SSVEPs at that frequency.

There were 56 letters per stream in a trial spanning 14 s (56 × 4 Hz = 14 s). Each trial contained a total of 5–12 (median = 9) target letters 'X' that could appear on either side. The onsets of consecutive X's were separated by at least 1 s (3 other letters in between) in order to allow for unambiguous assignment of detection responses to preceding 'X's. The entire experiment consisted of 200 trials (10 blocks of 20 trials each) presented in random order. There were 100 attend-left and 100 attend-right trials. In each of these conditions a total of 896 'X's were displayed, of which exactly half were displayed on each side. To measure the time-course of attention after cue-onset, the onsets of these target letters was controlled so that exactly four 'X's appeared in each of the 56

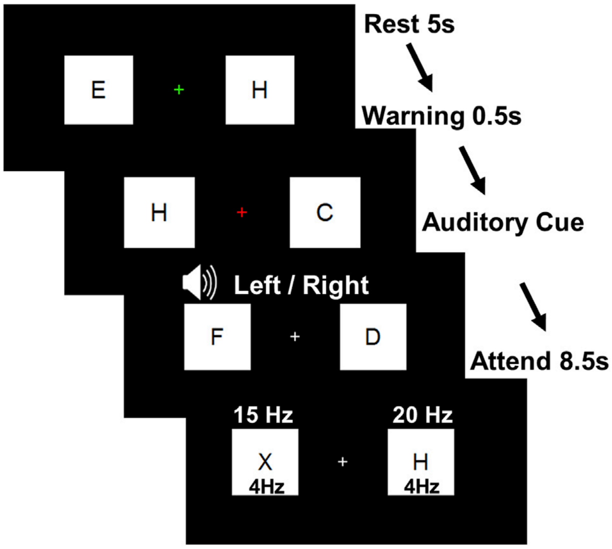

Fig. 1. Display configuration (not to scale) and trial sequence in Experiment 1. Black letter sequences changing at 4 Hz were superimposed on white flickering squares. Participants covertly attended to the cued letter stream and responded to targets ('X') during 8.5 s 'attend' periods, while ignoring the other stream.

letter positions for each side and each attentional condition over the entire experiment. Thus, a total of 352 ‘X’s appeared in the 22 letter positions (5.5 s) of the rest and warning period and 544 in the 34 letter positions of the attend period (8.5 s) across the two sides and two attentional conditions.

After each block participants received feedback on their performance for that block. The responding hand was switched halfway through the experiment with the initial responding hand counterbalanced between participants. Prior to data collection, participants completed two training blocks that contained half as many trials as the experimental blocks. Participants received auditory feedback during training (hits: high beep; false alarms & misses: low beep).

2.1.3. *Data analysis*

2.1.3.1. Behavioural data. Hits and false alarms were defined as responses occurring within 250–850 ms after onset of target letters ‘X’ in the cued or non-cued letter stream, respectively. Trials with horizontal eye-movements were rejected from all behavioural data analyses. To obtain the time-course of behavioural performance as a function of cue-target interval, hits, false alarms, and hit reaction times across the 56 letter positions (relative to cue onset) were subjected to a non-parametric Gaussian Kernel Smoothing Regression procedure (Nadaraya, 1964; Watson, 1964) for attend left and right conditions and for each participant separately. This procedure estimates a smooth curve from discrete data points through a locally weighted average over the data in a moving Gaussian window (full-width-at-half maximum = 179.4 ms; same temporal resolution as the Gabor filters used to quantify alpha and SSVEP time-courses; see below). The obtained hit rates, false alarms, and reaction times were then collapsed over attend-left and attend-right conditions (Fig. 2).

2.1.3.2. EEG recordings & data processing. Participants were seated in an electrically shielded chamber. Brain electrical activity was recorded at a sampling rate of 256 Hz from 64 Ag/AgCl electrodes mounted in an elastic cap using an ActiveTwo amplifier (BioSemi, Amsterdam, The Netherlands). To enhance the spatial sampling of lower occipital locations, electrode positions were modified from the manufacturer’s default 10–20 setup by moving electrodes from positions T7/8 and F5/6 to positions PO9/10 and I1/2. Vertical eye movements and blinks were monitored with a bipolar montage positioned above and below the left eye (vertical electrooculogram). Horizontal eye movements were monitored with a bipolar outer canthus montage (horizontal electrooculogram).

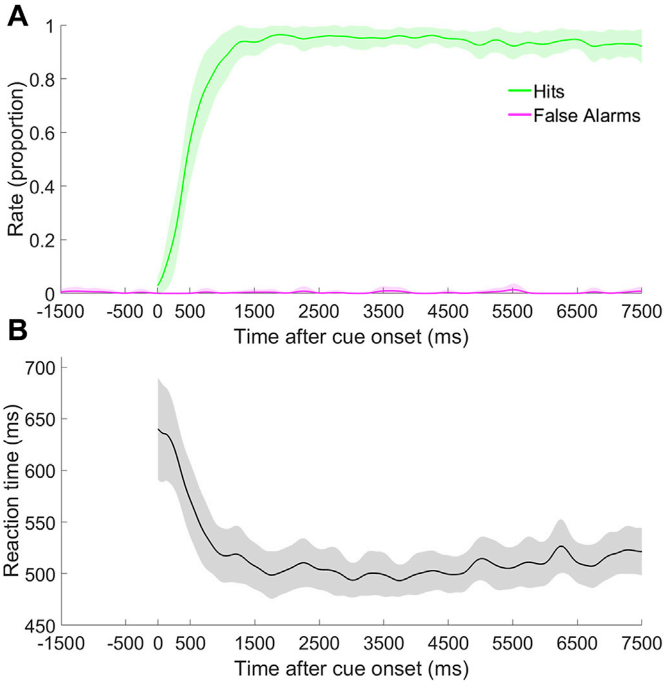

Fig. 2. Behavioural performance in Experiment 1. (A) Time-courses of Hits, False Alarms, and (B) Reaction Times as a function of cue-target interval obtained by kernel smoothing regression. Time zero is cue onset. Shaded areas are 95% confidence intervals.

The EEG data were processed using the EEGLAB toolbox (Delorme and Makeig, 2004) in combination with custom-made procedures in MATLAB (The MathWorks, Natick, MA). One hundred 10.5 s epochs per condition were extracted for each participant, ranging from −2.5 s (i.e. before cue onset) to 8 s after cue onset). All epochs were detrended (removal of linear trends) and those containing blinks or eye movements were rejected. The remaining epochs were subjected to an automated statistical control of artefacts in dense array studies (SCADS; Junghöfer et al., 2000) procedure. It uses a combination of trial exclusion and channel approximation for contaminated channels based on statistical parameters of the data. The final rejection rate was 42.0% of all epochs (attend left: 41.3%, range = 20.0%–61.0%; attend right: 42.4%, range = 18.0%–63.0%). All remaining epochs for each participant were then subjected to a scalp current density (SCD) transformation (Perrin et al., 1989). Compared to standard EEG references (e.g. averaged mastoids/earlobes or average reference), SCDs provide higher spatial resolution, correspond better with underlying cortical generators, and are reference-free (Kayser and Tenke, 2015).

2.1.3.3. Alpha band. To determine electrode sites with the highest alpha-band amplitudes for subsequent time-course analysis, amplitudes were calculated over a long time-window (1.5 s–7.5 s post-cue) using a Fourier transform. The beginning of this time-window (1.5 s) reflects a conservative estimate of the time when attentional shifting should have stabilized (Egeth and Yantis, 1997), while the ending (7.5 s) corresponds to the end of the analysed time-course data (see alpha time-course analysis below). Alpha amplitudes were calculated as the average of the absolute of the complex Fourier coefficients for all frequencies between 8.1 and 11.9 Hz for each trial separately and then averaged across trials (i.e. non-phase-locked amplitudes). This approach excludes the harmonics of the 4 Hz SSVEP letter switch rate at 8 Hz and 12 Hz. Trial-averaged alpha amplitudes peaked at parieto-occipital electrodes ipsilateral to attended locations (Fig. 3A). Accordingly, two symmetrical lateral clusters of three electrodes were selected for further analysis (PO3/PO4, PO7/PO8, and O1/O2). These electrode clusters are identical to those used by Kelly et al. (2006) to quantify alpha.

Time-courses of alpha amplitudes for both attentional conditions for each of the two electrode clusters were calculated using Gabor filters (Gabor, 1946). Thirty-nine Gabor filters with centre frequencies ranging from 8.1 Hz to 11.9 Hz in steps of 0.1 Hz were applied to each single epoch. All filters had the same frequency resolution of ±1.23 Hz full-width-at-half-maximum (FWHM), which corresponds to a temporal resolution of ±179.4 ms FWHM. The resulting amplitude time-courses were averaged across epochs, the three electrodes of each cluster, and the 39 centre frequencies to obtain the time-course of non-phase-locked alpha amplitudes for each attentional condition and electrode cluster, separately. Further, the data were re-scaled relative to a pre-cue baseline from −1.5 to −0.5 s, by dividing each data point by the mean amplitude over that baseline for each participant in each condition. This ensures that changes in alpha amplitude are represented relative to baseline.

Modulations of alpha amplitudes showed an equivalent pattern between attend left/right conditions in contra- and ipsilateral electrode clusters (Fig. 3C) and were therefore collapsed for conditions in which attention was directed to the contra and ipsilateral hemifield, separately (Fig. 3D). The relative amplitudes of the resulting alpha time-courses

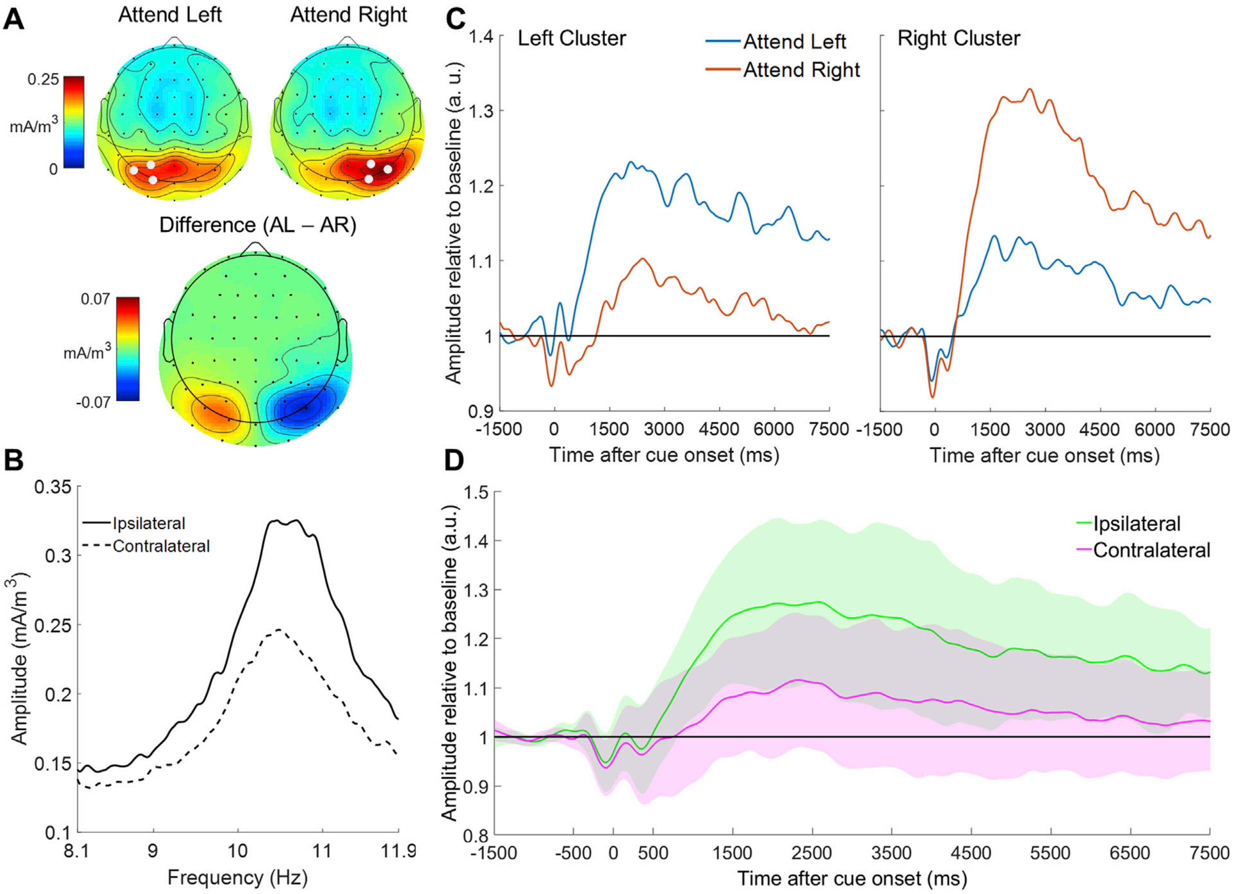

Fig. 3. Alpha band amplitudes in Experiment 1. (A) Grand mean scalp current density map of alpha amplitudes (averaged 1.5–7.5 s post-cue) for attend-left and attend-right conditions and their difference. Alpha amplitudes peak at parieto-occipital electrodes ipsilateral to the attended stimulus. Electrode clusters used for further analysis are indicated by grey dots. (B) Non-phase-locked spectra over the alpha-band (averaged 1.5–7.5 s post-cue; zero-padded to 2^{14} points). Amplitudes are higher at the cluster ipsilateral than contralateral to the attended stimulus. (C) Time-courses of alpha amplitudes after the attention directing cue (time zero). (D) Grand-average alpha time-course collapsed across left and right electrode clusters. The black line is the baseline. Shaded areas are 95% confidence intervals.

were averaged from 1.5 s to 7.5 s post-cue[1] and compared with 2-tailed t-tests against 1.0 (mean of the baseline after rescaling) to determine if they differed from baseline. The averaged ipsi- and contralateral amplitudes (averaged over 1.5 s–7.5 s post-cue) were then compared with a 2-tailed *t*-test.

2.1.3.4. Steady-state visual evoked potentials. To compute phase-locked SSVEP amplitudes, epochs were averaged for attend-left and attend-right conditions separately prior to time-frequency analysis. Topographies of SSVEP amplitudes at the background flicker rates (15 Hz & 20 Hz) and the letter switch rate (4 Hz) computed by Fourier transformation over the time-window of 1.5 s–7.5 s post-cue exhibited clear parieto-occipital peaks at the stimulation frequencies (Fig. 4A). Clusters were chosen to capture the peak activity at each SSVEP frequency. The central cluster (O1, Oz, & O2) captured 15 and 20 Hz in both conditions. Amplitudes at 4 Hz showed pronounced peaks contralateral to the attended stimulus. Therefore, they were measured at two symmetrical lateral clusters (left cluster: P7, P9, & PO7; right cluster: P8, P10, & PO8).

Attentional modulation at 15 and 20 Hz was less robust than expected (see Results), therefore time-course analysis of SSVEPs was performed only for 4 Hz signals. The latter were quantified with a single Gabor filter centred at 4.0 Hz with the same width as for behavioural and alpha time-course quantification (frequency resolution: ±1.23 Hz FWHM; temporal resolution: ±179.4 ms). Amplitudes were re-scaled relative to a baseline from −1.5 to −0.5 s. Attentional modulation at 4 Hz was equivalent for attend-left and attend-right trials, with the two lateral electrode clusters exhibiting higher amplitudes when attention was directed to the contralateral stimulus. Hence, time-courses at 4 Hz were collapsed across attend-left and attend-right trials for contra and ipsilateral to the attended stimulus electrode clusters separately (Fig. 4C). Averaged SSVEP amplitudes (1.5 s–7.5 s post-cue) in attended and unattended time-courses were compared against baseline with 2-tailed t-tests against 1.0 (mean of baseline after re-scaling). Then, a 2-tailed *t*-test compared the averaged attended and unattended amplitudes to determine if they differed.

2.1.3.5. Time-course of attentional modulation. To compare the time-course of attentional modulation between the different measures (alpha, SSVEP, hit rates), we computed latencies of the attentional shift for each measure separately. Reaction times were omitted from this analysis as the steep gradient in hit rates during the attention shift limited the number of data points for estimating hit RTs during the shift (see Fig. 2). We defined the latency as the first time-point at which half the difference between cue-onset (time 0 s) and post-shift asymptote (averaged over 1.5 s–7.5 s) was reached. For SSVEP and alpha amplitudes, this computation was performed on the difference wave of attended and unattended conditions. To obtain robust latency estimates, we employed a resampling approach for statistical comparison rather than computing

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[1] The employed Gabor filter was implemented by means of convolution which produces edge artefacts at the beginning and the end of the epoch. Statistical analysis excluded the last 0.5 s of the time-courses to prevent contamination by these edge artefacts.

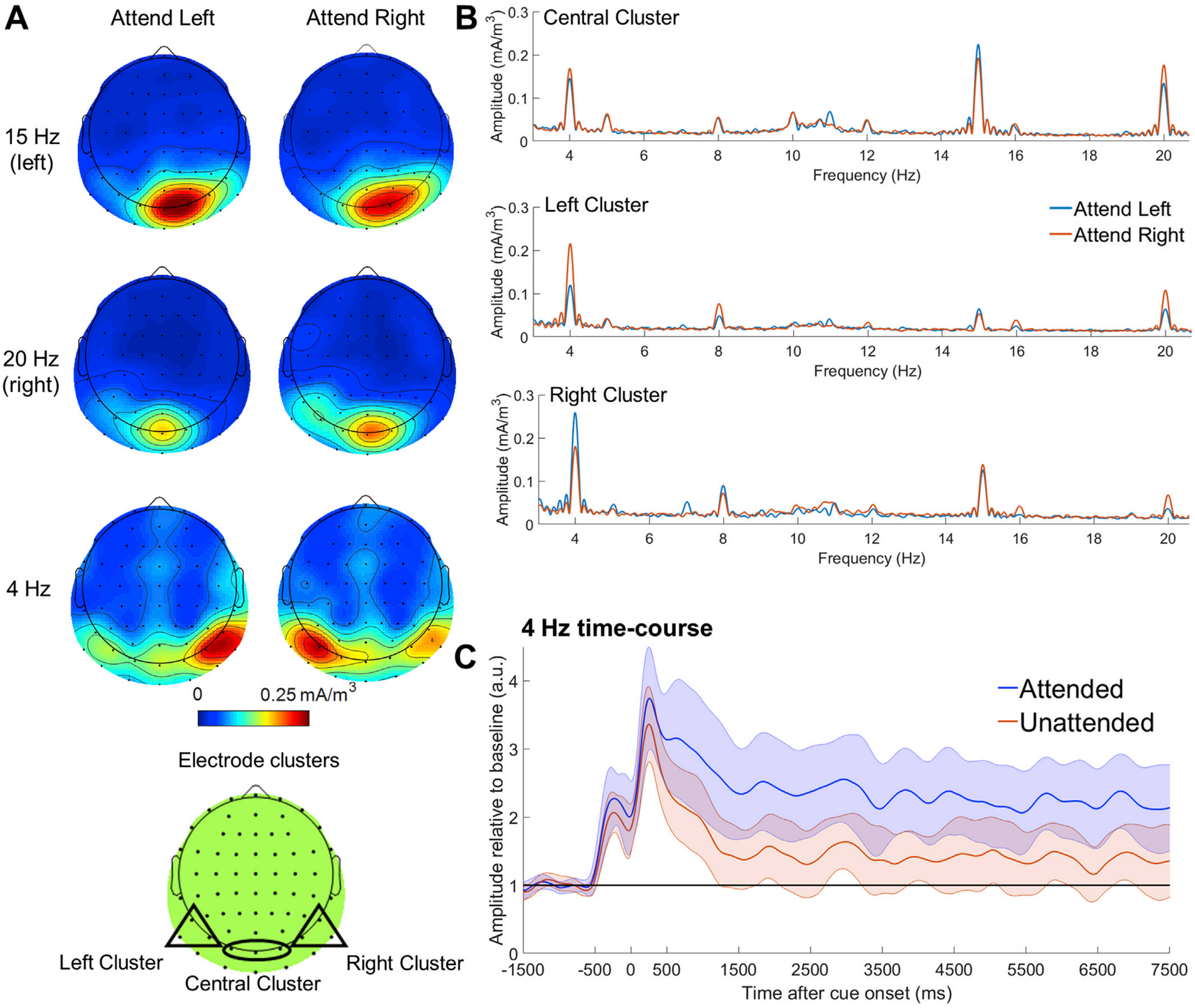

Fig. 4. SSVEP amplitudes in Experiment 1 (A) Grand mean scalp current density maps of SSVEP amplitudes at 15, 20, and 4 Hz (averaged 1.5–7.5 s post-cue). 4 Hz SSVEP amplitudes peak at parieto-occipital electrodes contralateral to the attended stimulus. (B) Phase-locked spectra (averaged 1.5–7.5 s post-cue; zero-padded to 2^{14} points) for the three electrode clusters (see the electrode montage) and the two attentional conditions. Clear peaks are localised at the letter switch frequency at 4 Hz and its harmonics and at the flicker frequencies (15 Hz and 20 Hz) of the background squares. The alpha peak in the non-phase locked spectrum (Fig. 3B) is strongly attenuated. (C) Time-course of 4 Hz SSVEP amplitudes collapsed across clusters for conditions where the contralateral stimulus was attended or unattended. Shaded areas are 95% confidence intervals. Time zero is cue onset. The black line is the baseline.

latencies for each participant independently. One participant without clear attentional modulation in alpha band amplitudes was excluded from all measures, leaving a sample size of 15. We drew 10000 samples of 15 participants from the original sample with replacement and computed the latency for each of the three measures for the mean across participants for each of these samples. An additional four participants exhibited a reversed alpha effect (i.e. alpha amplitudes were higher contralateral to the attended location than to the ipsilateral location). This reverse effect is not in line with the proposition that ipsilateral alpha-enhancement is a mechanism for distractor suppression. Nevertheless, as these participants still exhibited an alpha effect for which a latency can be estimated, we included them in the resampling. Their alpha difference waves were multiplied by −1.0 prior to resampling to account for the opposite direction of the effect.

The resampling resulted in 10000 sets of three latencies (one per measure) so that each set was derived from the same generated sample. 95% confidence intervals around the median were computed as the 250th and 9751st sorted latency values for each measure. Lastly, pairwise differences were taken between latency sets in each measure and 95% confidence intervals around each median difference were obtained as above.

2.2. Experiment 2

Surprisingly, SSVEPs elicited by the flickering backgrounds in Experiment 1 did not exhibit robust attentional modulation, unlike that observed in previous studies (e.g. Morgan et al., 1996; Kelly et al., 2005). However, we found strong attentional modulation of 4 Hz SSVEPs elicited by the letter switches. As the letter switch rate was the same on both sides, we were unable to separate SSVEPs elicited by the letter switches on the left and right side by frequency as we could for the SSVEPs elicited by the background flicker. Instead, the 4 Hz signals were analysed separately over the left and right hemisphere, assuming that these were mainly driven by the contralateral stimulus. This approach is limited in that we cannot be certain that the separation of the contralateral responses is perfect (i.e. the ipsilateral stimuli may have contributed to these signals, too). Therefore, we conducted a second experiment with different letter switch rates on the left (6 Hz) and right (4 Hz) side to verify our findings under conditions where SSVEPs can unambiguously be attributed to the different stimuli. Experiment 2 was identical to Experiment 1 except for the differences described below.

2.3. *Participants*

Twenty-four participants (self-reported: 8 males, 4 left-handed, 1 ambidextrous, aged: 19–38 years, median age = 23, with normal or corrected-to-normal vision) volunteered to take part in Experiment 2. Four participants were excluded from all analyses due to excessive artefacts in their EEG data (less than 40% trials remaining after artefact rejection in at least one condition). Another participant was excluded due to poor task performance (average hit rate <55% in both conditions), leaving a final sample size of nineteen.

2.4. *Stimuli and procedure*

In contrast to Experiment 1, the letter streams switched asynchronously at different frequencies to elicit distinct SSVEPs (Fig. 5). In order to allow for more trials, the duration of each individual trial was shortened to 8.5 s. The experiment had 300 trials (10 blocks of 30 trials). There were 150 attend-left and 150 attend-right trials, randomly presented across the experiment. Additionally, to avoid eliciting visual potentials to the 'rest' and 'warning' colour-changes of the fixation cross, these were eliminated and instead the end of the trial was indicated by an auditory cue saying "stop".

Letters in the left stream switched at 6 Hz (51 letters per trial), while letters in the right stream switched at 4 Hz (34 letters per trial). A median of 5 (range: 3–8) 'X's occurred per trial across both letter streams. A total of 714 'X's occurred per stream throughout the experiment. A target letter 'X' occurred in each letter position 14 times for the faster (6 Hz) stream on the left and 21 times for the slower (4 Hz) stream on the right over the course of the experiment. The onsets between consecutive 'X's were separated by at least 1 s irrespective of whether they occurred within the same or in opposite streams.

2.5. *Data analysis*

150 epochs per condition were extracted for each participant, ranging from −2.0 s before to 6.5 s after cue onset. The average rejection rate was 43.4% of all epochs (attend left: 45.0%, range = 32.0%–65.3%; attend right: 42.3%, range = 22.0%–55.3%).

Topographical distributions of alpha (Fig. 7A) and SSVEP (Fig. 8A) amplitudes were computed by a Fourier transform over the time-window from 1.5 to 5.0 s post-cue. SSVEP amplitudes at 4 and 6 Hz elicited clear peaks contralateral to the driving stimulus. Gabor filters for quantifying time-courses of non-phase-locked alpha-band amplitude (Fig. 7C) and phase-locked SSVEP amplitude (Fig. 8C) had a narrower frequency resolution of ±0.8 Hz FWHM (temporal resolution ±275.8 ms) than in Experiment 1 in order to avoid crosstalk between 4 and 6 Hz SSVEP frequencies. The baseline ranged from −1 to −0.7 s before the cue. Kernel smoothing regression of behavioural data was computed using the same temporal resolution of ±275.8 ms. The time-courses of behavioural data, alpha, and SSVEPs were analysed in a time-window from −1 s to 5.0 s after cue-onset.

2.5.1. *Time-course of attentional modulation*

One participant without a meaningful ipsi-contralateral alpha difference was excluded from all measures, leaving a sample size of eighteen for this analysis. Another participant exhibited a reversed alpha effect (i.e. contralateral alpha amplitudes were higher than ipsilateral upon visual inspection) and was included by multiplying alpha amplitudes by −1.0 before resampling.

3. Results

3.1. *Experiment 1*

3.1.1. *Behavioural performance*

Performance in the target detection task was high (Fig. 2A) with an average hit rate of 88.3% (range: 75.3%–97.6%; SD = 5.8%) over the

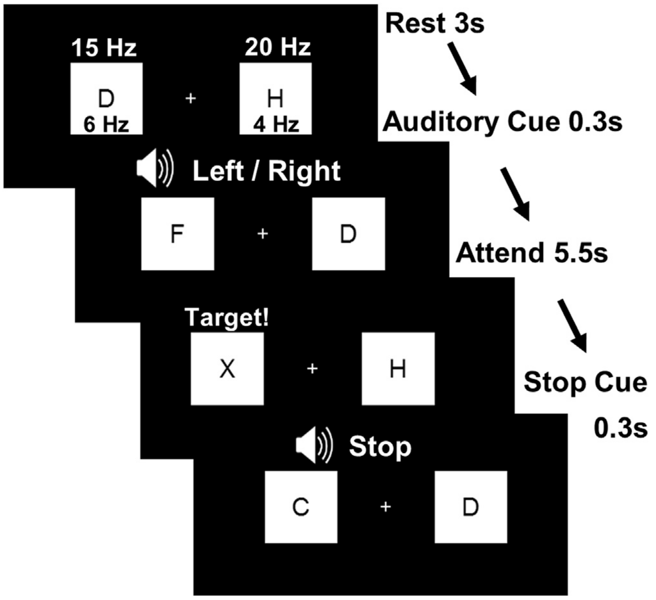

Fig. 5. Display configuration (not to scale) and trial sequence in Experiment 2. Letter sequences changing 6 (left) & 4 (right) Hz were superimposed on flickering squares. Participants covertly attended to the cued letter stream and responded to targets ('X') during 5.5 s 'attend' periods, while ignoring the other stream.

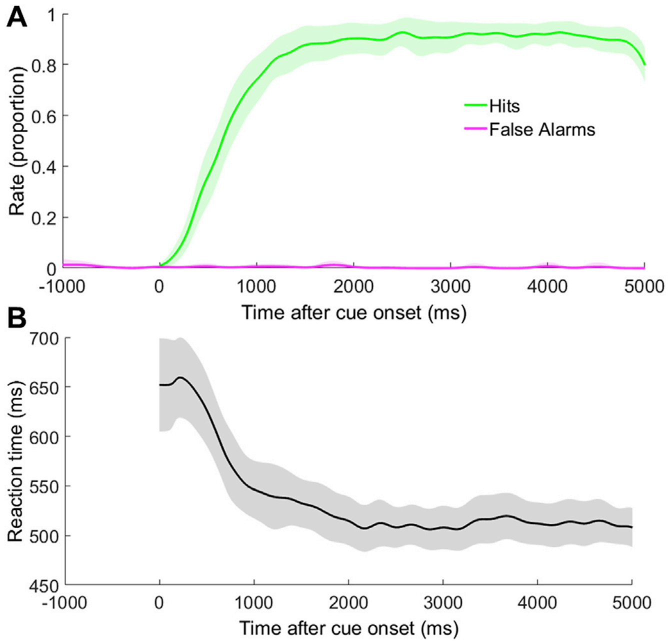

Fig. 6. Behavioural performance in Experiment 2. (A) Time-courses of Hits, False Alarms, and (B) Reaction Times as a function of cue-target interval obtained by kernel smoothing regression. Time zero is cue onset. Shaded areas are 95% confidence intervals.

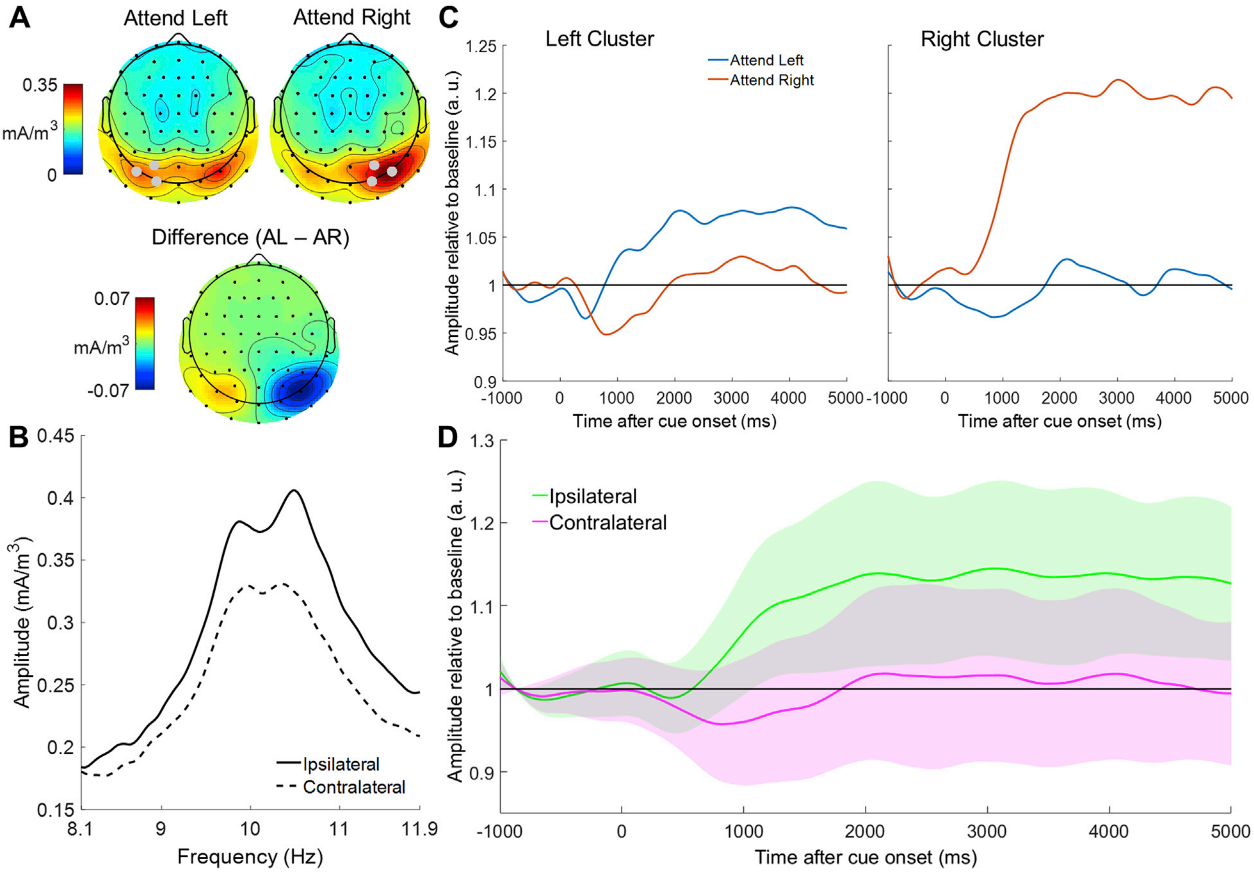

Fig. 7. Alpha band amplitudes in Experiment 2. (A) Grand mean scalp current density maps of alpha amplitudes (averaged 1.5–5 s post-cue) for attend-left and attend-right conditions and their difference. Alpha amplitudes peak at parieto-occipital electrodes. Electrode clusters used for further analysis are indicated by grey dots. (B) Non-phase-locked spectra over the alpha-band (averaged 1.5–7.5 s post-cue; zero-padded to 2^{14} points). Frequencies are higher at the cluster ipsilateral than contralateral to the attended location. (C) Time-courses of alpha amplitudes after the attention directing cue (time zero). (D) Grand-average alpha time-course collapsed across left and right electrode clusters. Time zero is cue onset. The black line is the baseline. Shaded areas are 95% confidence intervals.

time window from 0.0 to 7.5 s post-cue, and did not differ between the left and right side ($t(15) = 0.67$, $p = .51$, $d = 0.10$). Hit reaction times averaged over the same time-window were 517 ms (range: 491–647 ms; SD = 31.4 ms) and were slightly faster (~14 ms) for the right than for the left side ($t(15) = 3.10$, $p = .007$, $d = 0.42$). False alarms were very rare. The maximum false alarm rate at any time-point between 1.5 s pre-cue to 7.5 s post-cue (averaged over participants and over attend-left and attend-right conditions) was 1.70%.

3.1.2. *Alpha band*

Alpha amplitudes (averaged 1.5–7.5 s post-cue) peaked at parieto-occipital electrodes ipsilateral to attended locations (Fig. 3A) and were higher at the right compared to the left cluster ($t(15) = 3.0$, $p = .01$, $d = 0.21$). They were enhanced relative to baseline (−1.5 to −0.5s) ipsilateral to the attended side ($t(15) = 2.93$, $p = .01$, $d = 1.04$) but not on the contralateral side ($t(15) = 1.10$, $p = .30$, $d = 0.38$; Fig. 3D). One subject exhibited strong bilateral post-cue increases of alpha amplitudes: this is the main reason why grand-mean contralateral post-cue alpha amplitudes as depicted in Fig. 3D are consistently above baseline despite this difference not being significant. Importantly, the alpha amplitude ipsilateral to attended stimuli was substantially higher than contralateral ($t(15) = 3.02$, $p = .009$, $d = 0.53$).

3.1.3. *Steady-state visual evoked potentials*

Unexpectedly, SSVEP amplitudes elicited by the background flicker rate at 15 Hz measured at the central cluster did not show attentional modulation ($t(15) = 0.94$, $p = .36$, $d = 0.23$), but amplitudes at 20 Hz did ($t(15) = 3.50$, $p = .004$, $d = 0.45$). Pronounced attentional modulation of SSVEP amplitudes at the letter switch rate of 4 Hz was observed: these were higher contralateral than ipsilateral to the attended side (left cluster: $t(15) = 5.13$, $p < 2 \times 10^{-4}$, $d = 0.92$; right cluster: $t(15) = 6.33$, $p < 2 \times 10^{-5}$, $d = 0.57$). Therefore, 4 Hz SSVEP amplitudes were selected for further time-course analysis.

Time-courses of SSVEP amplitudes at 4 Hz exhibited visible enhancement in both the attended (contralateral to the attended stimulus) and unattended (contralateral to the unattended stimulus) conditions around the times of the warning and the cue (Fig. 4C). Averaged over a time-window from 1.5 s to 7.5 s post-cue, 4 Hz SSVEP amplitudes were significantly enhanced relative to baseline (−1.5 s to −0.5 s) when the contralateral stimulus was attended ($t(15) = 4.64$, $p < 4 \times 10^{-4}$, $d = 1.64$), but a confident argument for enhancement when the contralateral stimulus was unattended cannot be made ($t(15) = 2.01$, $p = .06$, $d = 0.71$). Nevertheless, the direction of change for this cluster was an increase in amplitudes, rather than a decrease as the alpha suppression hypothesis would predict. Importantly, SSVEP amplitudes in the attended time-course were higher than in the unattended in the same time window ($t(15) = 3.90$, $p = .002$, $d = 0.90$).

3.1.4. *Latencies*

If alpha activity reflects an active mechanism for reallocating attention, then changes in the alpha band following an attention directing cue should precede changes in other measures of selective attention. In order to test this, the latencies of attentional modulation of the alpha band (ipsilateral – contralateral), SSVEP amplitudes (attended – unattended), and hit rates were compared by a re-sampling approach (see Data analysis in the Method section; Fig. 9).

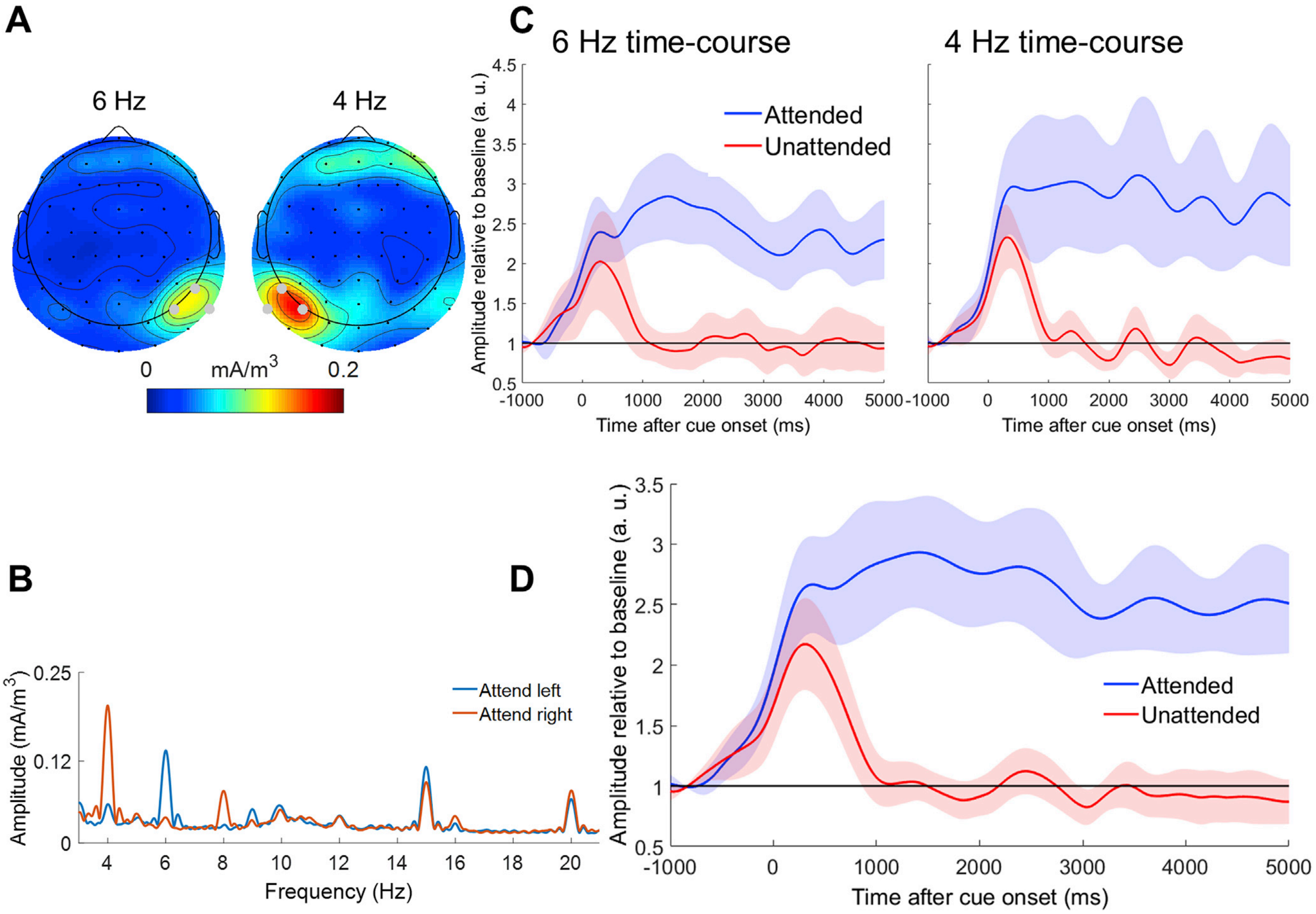

Fig. 8. SSVEPs amplitudes in Experiment 2. (A) Grand mean scalp current density maps of SSVEP amplitudes at 6 and 4 Hz (averaged 1.5–5 s post-cue). Amplitudes peak at parieto-occipital electrodes contralateral to the driving stimulus. Electrode clusters used for further analysis are indicated by grey dots. (B) Phase-locked amplitude spectra (averaged 1.5–5 s post-cue; zero-padded to 2^{14} points) of the average of both electrode clusters for both attentional conditions. Clear peaks are localised at the letter switch frequencies of 6 Hz, 4 Hz, their harmonics, and at the flicker frequencies of the background squares at 15 Hz and 20 Hz. (C) Time-courses of SSVEP amplitudes relative to baseline at the electrode cluster contralateral to the driving stimulus. SSVEP amplitudes at 6 and 4 Hz show equivalent patterns. (D) Grand-average SSVEP amplitude time-course collapsed across 6 and 4 Hz. Shaded areas are 95% confidence intervals. Time zero is cue onset. The black line is the baseline.

Hit rates increased sharply post-cue. The median latency of this post-cue effect was 445 ms (95% CI: 375–555 ms). The latency of SSVEP attentional modulation was 414 ms (95% CI: 238–660 ms), while that of alpha band attentional modulation was 633 ms (95% CI: 520–766 ms).

Pairwise comparisons of the latencies of attention effects on the various measures revealed that attentional modulation of hit rates and SSVEPs preceded attentional modulation of alpha band by a median difference of 180 ms (95% CI: 51–340 ms, $p = .009$) and 207 ms (95% CI: 27–391 ms, $p = .03$), respectively. The latencies of SSVEPs did not differ from those of hit rates (median difference: 35 ms, 95% CI: –231 to 238 ms, $p = .80$).

3.2. Experiment 2

3.2.1. Behavioural performance

The average hit rate (Fig. 6A) in detecting the targets was 79.0% (range: 55.0%–89.2%; SD = 8.20%; averaged 0–5 s post-cue). Hit rates tended to be slightly lower for targets in the faster (6 Hz; mean = 77.0%, SD = 10.1%) than in the slower (4 Hz; mean = 80.1%, SD = 8.0%) stream ($t(18) = 2.30$, $p = .04$, $d = 0.41$). Hit reaction times averaged over the same time-window were 536 ms (range: 456–605 ms; SD = 44 ms). The maximum false alarm rate at any time point between −1 s and 5 s averaged across participants was 1.40%.

3.2.2. Alpha band

Alpha amplitudes (averaged 1.5–5 s post-cue) peaked at parieto-occipital electrodes (Fig. 7A). As in Experiment 1, alpha amplitudes ipsilateral to the attended location were higher at the right compared to the left cluster ($t(18) = 2.43$, $p = .03$, $d = 0.34$).

The time-courses of alpha amplitudes were equivalent for the two electrode clusters (Fig. 7C) and therefore collapsed across clusters prior to statistical analysis. Post-cue alpha amplitudes (averaged 1.5–5 s) were enhanced relative to baseline (−1 to −0.7 s) ipsilateral to the attended side ($t(18) = 2.82$, $p = .01$, $d = 0.92$) but did not differ on the contralateral side ($t(18) = 0.20$, $p = .90$, $d = 0.06$; Fig. 7D). Importantly, alpha amplitudes ipsilateral to the attended location were higher than contralateral (averaged 1.5–5 s; $t(18) = 6.20$, $p < 9 \times 10^{-6}$, $d = 0.61$).

3.2.3. Steady-state visual evoked potentials

SSVEP amplitude time-courses at 6 Hz and 4 Hz exhibited similar patterns (Fig. 8C) and were thus collapsed across frequencies. As in Experiment 1, there was enhancement of both the attended and unattended time-courses around the onset of the cue. The attended amplitude averaged over time (1.5–5 s) showed a pronounced enhancement relative to baseline (−1 to −0.7 s; $t(18) = 9.0$, $p < 7 \times 10^{-8}$, $d = 2.90$), while the unattended did not differ ($t(18) = 0.81$, $p = .43$, $d = 0.30$). Importantly, SSVEP amplitudes were higher when the eliciting stimulus was attended

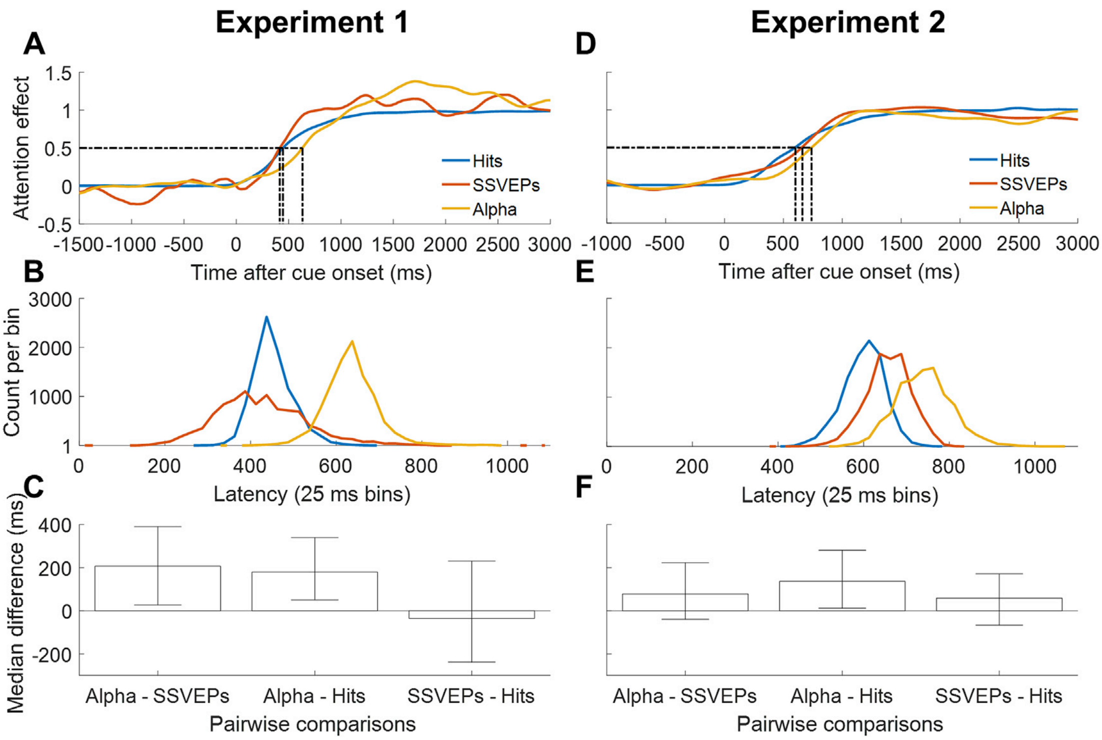

Fig. 9. Time-course of attentional modulation. Time-courses of hits, SSVEPs, and alpha obtained through re-sampling and re-scaled to asymptote in (A) Experiment 1 (asymptote: 1.5–7.5 s) and (D) Experiment 2 (asymptote: 1.5–5 s). Dotted lines indicate the estimated latency (half the difference between time 0 and averaged asymptote) of attentional modulation on each measure. Distributions of 10000 re-sampled latencies partitioned in 44 bins of 25 ms in (B) Experiment 1 & (E) Experiment 2. Pairwise comparisons between the measures show that attentional modulation of alpha did not precede that of hits and SSVEPs in both experiments. Latencies of hits and SSVEPs preceded that of alpha in (C) Experiment 1. Attentional modulation of hits preceded that of alpha in (F) Experiment 2. Error bars reflect 95% confidence intervals of the difference between measures.

compared to when it was unattended (averaged 1.5–5 s post-cue; $t(18) = 8.10$, $p < 3 \times 10^{-7}$, $d = 2.80$).

3.2.4. *Latencies*

The latencies of attentional modulation of the alpha band (ipsilateral − contralateral), SSVEP amplitudes (attended − unattended), and hit rates, were compared by re-sampling as in Experiment 1 (Fig. 9). Hit rates improved steadily post-cue compared to Experiment 1. The median latency of this effect was 602 ms (95% CI: 496–684 ms). This is about 160 ms slower than in Experiment 1, which may in part be due to the absence of the trial-by-trial warning before the cue. The latency of the SSVEP attentional modulation was 661 ms (95% CI: 547–750 ms), while that of the alpha band was 739 ms (95% CI: 617–875 ms).

Pairwise comparisons between the 10000 re-sampled latencies of attention effects on the various measures revealed that attentional modulation of hit rates preceded attentional modulation of alpha band by a median difference of 137 ms (95% CI: 12–282 ms, $p = .03$). The latencies of attentional modulation of SSVEPs did not differ to those of alpha (median difference: 79 ms, 95% CI: 39 to 223 ms, $p = .20$) and hit rates (median difference: 59 ms, 95% CI: 66 to 172 ms, $p = .40$).

4. Discussion

We examined the hypothesis that alpha band activity reflects an active mechanism for distractor suppression in two EEG experiments. If there were such a causal link, then increases in alpha band activity should precede suppression of distractors at the corresponding location. We replicated previous findings (Kelly et al., 2006) of an increase in alpha band amplitude ipsilateral to the attended location, which is the finding that prompted the alpha suppression hypothesis. However, the predicted effect of this hypothesized mechanism did not occur: we observed enhanced processing of attended stimuli (as indexed by SSVEP amplitudes) rather than suppressed processing of unattended stimuli that was not preceded by changes in the alpha band.

The observed effects in our two experiments fundamentally conflict with the notion that alpha band activity reflects a key mechanism for allocating selective attention and more specifically mediating distractor suppression. First, as noted above, selective attention enhanced the representation of attended stimuli rather than suppressing unattended stimuli, despite increases in alpha amplitude contralateral to the unattended side. Thus, attention modulated stimulus processing in the opposite hemisphere of the observed effects in the alpha band. Second, changes in the alpha band did not precede attentional modulation of stimulus processing. In fact, it was the other way around, with enhancements in attended stimulus processing and behaviour preceding alpha activity increases. This, once again, contradicts the predictions of the alpha suppression hypothesis. Third, attentional enhancement of stimuli on the task relevant side, as indexed by SSVEP amplitudes elicited at the letter switch rate, was around 100–200% of the baseline amplitude (Figs. 4C & 8D), whereas attentional enhancement of alpha band amplitudes was only around 10–30% (Figs. 3D & 7D). Expressed in terms of statistical effect sizes, the corresponding Cohen's d values are 1.6–2.9 for SSVEPs and 0.9–1.0 for alpha. Thus, attentional effects in the alpha band were about an order of magnitude smaller than attentional modulation of SSVEP in relative terms and were statistically less reliable. In itself, this last point does not rule out the alpha suppression hypothesis because causal chains of processing can be non-linear, but suggests that alpha effects are weaker, and at a minimum, additional mechanisms might be needed to explain attentional effects, if at all. The inconsistency of the pattern of these results with the alpha suppression hypothesis is further highlighted by the five participants (four in Experiment 1 and one in Experiment 2) showing a reversed alpha effect (i.e. contralateral alpha higher than ipsilateral) but equivalent behavioural and SSVEP data to other participants. In summary, in our two experiments and prior studies

(Müller et al., 1998; Kashiwase et al., 2012), target enhancement rather than distractor suppression is the predominant attentional effect on stimulus processing. Crucially, alpha band effects are too small, occur too late, and in the opposite hemisphere to where modulation of task relevant processing occurs. This makes them an implausible signature of a causal mechanism of selective attention. Changes in the alpha band did not precede attentional selection and are thus most likely a consequence of, rather than a mechanism for, attentional selection.

We challenge the interpretation of previous work in support of the alpha suppression hypothesis, but not the underlying data. In fact, our two experiments confirmed previous findings that alpha activity reflects the allocation of selective attention (Sauseng et al., 2005; Yamagishi et al., 2003; Kelly et al., 2006; Rihs et al., 2007; Samaha et al., 2016; Bacigalupo and Luck, 2019). However, considering our direct measures of attentional selection (hit rates and SSVEP amplitudes), the interpretation that these alpha effects reflect an active mechanism for attentional allocation becomes untenable. Initial evidence for the alpha suppression hypothesis was derived from the observation that alpha amplitudes in the cue-stimulus interval reflected the cued location (Worden et al., 2000). As these changes in the alpha band occurred prior to the onset of task relevant stimuli, they were interpreted to reflect anticipatory biasing of visual attention. However, the cue-stimulus interval in that study was fixed at 1000 ms and alpha band effects started after about 400 ms and peaked just before stimulus onset, which is much longer than behavioural estimates of the time needed to shift spatial attention derived from studies in which the cue-stimulus interval is varied to behaviourally sample the time-course of attention shifts (Müller and Rabbitt, 1989; Duncan et al., 1994; Müller et al., 1998; Andersen and Müller, 2010; Kashiwase et al., 2012). Thus, the alpha band effects reported in Worden et al. (2000) may have occurred after attention had shifted (as in the current set of experiments), although this cannot be ascertained as the study did not estimate the time-course of shifting attention through direct behavioural or electrophysiological measures. A similar argument can be made in the case of Kelly et al. (2006), where the claim that increases in alpha power reflect a mechanism for distractor suppression was made in absence of actual measures of distractor suppression. In summary, we attribute the conflict between our present findings and the alpha suppression hypothesis to unverified assumptions underlying the interpretation of previous studies. Our data fundamentally conflict with these assumptions and thus undermine the interpretations that rest upon them. Based on our present findings, we propose that the relationship between the alpha band and selective attention is that changes in the alpha band occur as a consequence of preceding shifts of attention. Our data does not allow us to conclude by which mechanism these attentional shifts are enacted, but we can exclude the possibility that it is due to the observed effects in the alpha band. To use a metaphor: (alpha) waves in a pond reflect where a rock fell into the water, but to propose that changes in the waves made the rock fall into that place in the pond inherently conflicts with the causality of the phenomenon.

Two recent studies provide converging evidence for independent attentional modulations of alpha-band and SSVEP amplitudes (Gundlach et al., 2020; Keitel et al., 2019). Interestingly, Gundlach et al. (2020) estimated that changes in the alpha band preceded those in SSVEPs after an attention-directing cue, which is the opposite of what we found. This might, however, be because of their use of a visual attention-directing cue, which would have elicited visual evoked potentials, which in turn would have affected their measures of alpha and SSVEPs in the early post-cue window. In our experiments, the use of auditory cues avoided such potential distortions, which might explain this difference. Keitel et al. (2019) showed that phase-locked SSVEPs presented within the alpha-band (10 & 12 Hz) and non-phase-locked alpha were modulated independently by assessing evoked and induced spectral analyses, respectively. Evoked SSVEP signals were increased for the attended versus unattended stimulus, but the opposite pattern was found for induced alpha-band activity. These findings are in line with our data, which was obtained with SSVEPs outside the alpha band. Taken together, these results also challenge the view that alpha oscillations represent a mechanism that controls attentional selection directly.

It is important to detail how potential crosstalk between SSVEPs and the alpha-band was avoided in our studies. This relied on two main principles. First, SSVEP frequencies (4 & 6 Hz and 15 & 20 Hz) were outside of the analysed alpha-band range (8.1–11.9 Hz). The harmonics at 8 and 12 Hz were at the edges of the analysed alpha-range, but there was no evidence to suggest that these harmonics contaminated the alpha signal. If such contamination had been present, then alpha amplitudes contralateral to the attended stimulus should have been enhanced close to the edges of the alpha-band compared to ipsilateral, which was not the case (see Figs. 3B and 7B). Second, as is commonly the case, we computed SSVEP amplitudes using evoked (phase-locked) spectral analyses, whereas alpha amplitudes were computed using induced (non-phase-locked) spectral analyses. Keitel et al. (2019) showed that alpha and SSVEP modulations were independent, even when, unlike in the current study, the signals overlapped in frequency space. Finally, a contamination of the alpha-band by SSVEPs should (at least partly) have masked the latency differences between these signals. In sum, there was no evidence that the current findings were affected by crosstalk between the alpha-band and SSVEPs.

An alpha-decrease was not observed in the current experiments. This was also the case in Kelly et al. (2006), who argued this might have been because of the constant visual stimulation reducing baseline alpha amplitudes, which in turn, could have limited further relative decreases. Given the similarity between our experimental designs, this could have been the case in our study, too. In addition, anticipatory alpha-decreases have typically been observed in tasks without distractors at unattended locations (e.g. Sauseng et al., 2005; Thut et al., 2006; Capilla et al., 2012), while in our study and in Kelly et al. (2006) targets at attended and distractors at unattended locations were presented together. Alpha-decreases might also depend on other task conditions, such as the timing of target appearance (for an extensive discussion, see Rihs et al., 2009). Anticipatory alpha-decreases dominated early post-cue, while alpha-increases dominated later during sustained spatial attention in that study. However, while the cue-to-target intervals in Rihs et al. (2009) were fixed, targets in our study were temporally unpredictable, which might also partly explain the lack of an alpha-decrease in our study.

Our results contradict the suggestion that alpha-enhancement is an active mechanism that causes distractor suppression, but they do not rule out other proposed role(s) of alpha oscillations. Mounting evidence argues that alpha oscillations are related to neural activation/inhibition (Klimesch, 2012). For example, the pulsed-inhibition hypothesis (Jensen et al., 2012) suggests that alpha exerts suppression in a phasic manner (Klimesch et al., 2007; Jensen and Mazaheri, 2010; Mathewson et al., 2011). An exemplar of this is that higher alpha amplitude is associated with lower neuronal firing rates so that firing rates are lowest at the peak of the alpha-cycle (Haegens et al., 2011). However, reduced alpha amplitudes can plausibly be a consequence of enhanced firing rates, yet would produce the observed correlational pattern (but see Spaak et al., 2012; Bonnefond and Jensen, 2015). Further, Buffalo et al. (2011) found that with attention, alpha amplitudes were suppressed only in the deep compared to superficial layers of visual areas V1 & V2 in rhesus monkeys. In V4, alpha was suppressed in both layers, but more strongly in the deep layer. These laminar differences suggest that alpha manifests differentially across and within areas, whereas the mere summation of these processes observed on the scalp with EEG may not fully reflect them. Nevertheless, we specifically tested the prominent claim that alpha amplitude itself reflects an attentional mechanism for distractor suppression (Kelly et al., 2006; Van Diepen et al., 2019) and did not focus on its phasic properties. Other authors have suggested that alpha oscillations may be related to post-perceptual processing stages, rather than the sensitivity of the sensory system (Chaumon and Busch, 2014). For example, pre-stimulus alpha power has been associated with the tendency to report a stimulus as present (independent of its physical presence), rather than modulating the sensitivity in visual discrimination (Limbach and Corballis, 2016). Further, pre-stimulus alpha power has also been related to subjective rather than objective visual task performance (Samaha et al., 2017; Benwell et al., 2017). While our data specifically contradict the alpha-suppression hypothesis, it remains unclear whether alpha oscillations may reflect such other potential functional role(s).

In comparing the estimated latencies of shifting attention from behavioural and electrophysiological measures, it is important to consider that the time-course of hit rates was indexed to the onset of stimuli, whereas SSVEPs reflect the processing of stimuli presented 100–150 ms earlier (Müller et al., 1998). Therefore, attentional modulation of SSVEPs in both our experiments occurred early enough to causally affect behavioural performance, in line with previous studies that found a close relationship between behavioural performance and SSVEPs (Müller et al., 1998; Andersen and Müller, 2010; Kashiwase et al., 2012). Alpha band amplitudes reflect ongoing oscillations rather than stimulus processing, and thus the above logic is hard to apply to the comparison with hit rates. However, the comparison between the two electrophysiological measures, SSVEPs and alpha, is unaffected by these considerations and unambiguously showed that attentional modulation of SSVEPs was not preceded by attentional modulation of alpha in both experiments. Importantly, we ensured that all latencies were estimated from measures that had the same temporal resolution. We used Gabor filters with a fixed width across all analysed frequencies, as opposed to Morlet wavelets, where temporal resolution scales directly with the analysed frequency. We also employed the same width of Gaussian windows in the time-course analysis of behavioural data in each experiment. In this way, estimated latencies from the different measures could be compared directly. Furthermore, by using a half-asymptote definition of latency, we adopted an approach that is unbiased by statistical power (unlike approaches such as determining onsets via running t-tests, which are biased towards earlier latencies with higher statistical power).

Unexpectedly, we did not consistently find robust attentional modulation of SSVEPs elicited by the flickering background squares. Compared to the seminal study by Morgan et al. (1996) which established the sensitivity of SSVEPs to attention, the background squares in our study (and in Kelly et al., 2006) were much larger in relation to the task-relevant letters. Selective attention might have been closely focused on the relevant letters, yielding a less consistent attentional modulation of the much larger background squares (see Wang et al., 2007). However, we found pronounced and consistent attentional modulation of the SSVEPs elicited by the shape changes of the letter streams at 4 and 6 Hz. The topographies of these SSVEPs also differed markedly, with the flickering squares eliciting SSVEPs with narrow peaks at central occipital electrodes and letter changes eliciting SSVEPs with more lateral peaks (see Figs. 4 and 8). These topographies are very consistent with SSVEP topographies in our previous work (e.g. Andersen et al., 2012; Adamian et al., 2019) and most likely correspond to sources in V1–V3 (background squares) and MT/LOC (letter shapes), respectively (see also Di Russo et al., 2007). Using closely intermingled stimuli, our previous studies also found strong attentional modulation in the electrode clusters corresponding to the earliest stages of cortical visual processing (V1–V3), which we did not observe here. This is consistent with prior work within the biased competition framework showing that attentional modulation is most pronounced when attended and unattended stimuli fall into shared receptive fields (Luck et al., 1997), which is more likely to happen in later visual areas with larger receptive fields.

In conclusion, the current study contradicts the hypothesis that increases in alpha amplitude reflect an active mechanism for distractor suppression. Although alpha amplitudes were enhanced in a sustained manner, this did not lead to a suppression of the processing of unattended stimuli, as indexed by steady-state visual evoked potentials (SSVEPs). Instead, selective attention robustly enhanced the processing of attended stimuli. In addition, attentional modulation of stimulus processing was not preceded by changes in the alpha band. Therefore, alpha amplitude effects are not a causal mechanism of selective attention. Amplitude changes in the alpha band did not occur before attentional selection and are thus most likely a consequence of it, rather than the mechanism responsible for its execution.

Data and code availability

All data and code are available from the authors upon reasonable request.

Declaration of competing interest

The authors declare no competing financial interests.

CRediT authorship contribution statement

Plamen A. Antonov: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review & editing, Visualization, Project administration. **Ramakrishna Chakravarthi:** Conceptualization, Methodology, Validation, Resources, Writing - review & editing, Supervision. **Søren K. Andersen:** Conceptualization, Methodology, Software, Validation, Resources, Writing - review & editing, Supervision, Project administration.

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