Facilitation and inhibition in attention: Functional dissociation of pre-stimulus alpha activity, P1, and N1 components

Slagter, Heleen; Prinssen, Sam; Leon C Reteig, Leon; Mazaheri, Ali

DOI:
10.1016/j.neuroimage.2015.09.058

Document Version
Peer reviewed version

Citation for published version (Harvard):
Slagter, H, Prinssen, S, Leon C Reteig, L & Mazaheri, A 2016, 'Facilitation and inhibition in attention: Functional dissociation of pre-stimulus alpha activity, P1, and N1 components', *NeuroImage*, vol. 125, pp. 25-35. https://doi.org/10.1016/j.neuroimage.2015.09.058

Facilitation and inhibition in attention: Functional dissociation of pre-stimulus alpha activity, P1, and N1 components

Slagter, H.A.†¶*, Prinssen, S.†, Reteig, L.C.†, & Mazaheri, A.°¶

† Department of Psychology, University of Amsterdam, Weesperplein 4, 1081XA, Amsterdam, the Netherlands

¶ Amsterdam Brain and Cognition, University of Amsterdam, Weesperplein 4, 1081XA, Amsterdam, the Netherlands

° School of Psychology, University of Birmingham, B15 2TT, United Kingdom

* To whom correspondence should be addressed: h.a.slagter@uva.nl, Department of Psychology, University of Amsterdam, Weesperplein 4, 1081 XA, Amsterdam, the Netherlands

Abstract

Attention – the ability to attend to some things while ignoring others – can be best described as an emergent property of many neural mechanisms, facilitatory and inhibitory, working together to resolve competition for processing resources and control of behavior. Previous EEG and MEG studies examining the neural mechanisms underlying facilitation and inhibition of stimulus processing typically used paradigms requiring alternating shifts of attention in the spatial domain, with stimuli occurring at both attended and unattended locations. These studies generally observed greater pre-stimulus alpha oscillations over task-irrelevant vs. relevant posterior regions and bilateral attentional modulations of early sensory processing. In contrast, in the current series of experiments, participants continuously attended to only one hemifield and stimuli were only presented at the attended location, affording us an opportunity to elucidate the inhibitory and facilitatory effects of attention in the brain in a context in which spatial relevance was fixed. We found that continuous attention to one hemifield did not modulate prestimulus alpha activity in ipsilateral regions but did result in a perfectly lateralized P1 attention effect to ipsilateral posterior regions. Moreover, we found a bilateral N1 effect. These findings suggest that pre-stimulus alpha activity, the P1 and the N1 reflect qualitatively different aspects of attention; While pre-stimulus alpha-band activity may reflect a top-down inhibitory mechanism that critically depends on functional competition between task-relevant and irrelevant sensory regions, the ipsilateral P1 effect may reflect stimulus-triggered blocking of sensory processing in irrelevant networks, and the N1 effect facilitation of task-relevant processing.

Key words

Attention, ERP, alpha, P1, brain, EEG

Highlights

- In this EEG study, participants continuously attended to only one hemifield
- With one side ever relevant, attention did not modulate prestimulus alpha activity
- Attention modulated the P1 only ipsilaterally, and the N1 bilaterally
- Prestimulus alpha activity, the P1 and N1 reflect different aspects of attention
- Attention is subserved by multiple inhibitory and facilitatory neural mechanisms

Introduction

A large body of research shows that attention – the ability to focus on task-relevant aspects of the environment while ignoring others – can facilitate goal-directed behavior by biasing sensory brain regions in advance to favor processing of relevant over irrelevant events. For example, prior to stimulus presentation, attention to a location in space (e.g., left) has been associated with greater alpha oscillatory activity (8-14Hz) over ipsilateral posterior brain regions (reflecting top-down inhibition of irrelevant networks) and reduced alpha activity over contralateral regions representing the to-be-attended location (or enhanced cortical excitability of relevant networks) (Worden et al., 2000; Thut et al., 2006). Moreover, visuospatial attention can modulate subsequent stimulus processing, as reflected in larger amplitudes of the early visual-evoked potentials P1 and N1 (Eason et al., 1969; Mangun and Hillyard, 1991). Notably, several studies suggest that these effects may reflect qualitatively different aspects of attention, with the P1 reflecting inhibition and the N1 amplification (Couperus and Mangun, 2010; Freunberger et al., 2008; Luck et al., 1994).

Yet, debate remains about the precise role of these different neural processes in selective attention. Some EEG studies show suppression by alpha activity when there is competition from distracting information (e.g., Worden et al., 2000; Kelly et al., 2006). Yet, other studies report pre-stimulus alpha increases in the absence of distractors (e.g., Rihs et al., 2007), leaving it unclear whether alpha activity reflects top-down inhibition that is dependent on competition for limited processing resources. The P1 attention effect has also been related to inhibition. According to the influential sensory gain model, this effect reflects suppressed sensory processing of unattended stimuli (Hillyard et al., 1998; Luck, 1995). Yet, recently, it was proposed that the P1 reflects the same functionality as alpha does, namely a top-down inhibitory process that modulates feed-forward sensory processing of both attended and unattended stimuli (Klimesch, 2011). In contrast to the sensory gain account in which greater inhibition should lead to suppressed visual processing and a concomitant smaller P1, in this account, greater inhibition should be associated with a larger P1.

The aim of the current series of EEG studies was to gain a better understanding of the functional significance of pre-stimulus alpha activity, the P1, and N1 within the context of visual spatial attention. To this end, participants covertly directed their attention to the same location during the entire experiment, and stimuli were only presented at the attended location. Thus, one hemifield was *always* relevant, while the other hemifield was *never* relevant. We reasoned that this consistency in relationship between hemifield and relevance

would allow us to better separate inhibitory and facilitatory effects of attention in the brain. In prior studies, participants typically switched between attending left and right, with stimuli occurring at both attended and unattended locations. This may have affected attentional control mechanisms, as it is well known that trial type probabilities and intermixed presentation of trial types can affect attention deployment (Eimer, 1996; Luck et al., 1990; Slagter et al., 2005). For example, if the currently relevant location was irrelevant in the previous trial (and hence the currently to-be-ignored location, relevant), this can affect how attention is deployed.

We specifically examined effects of continuous attention to one hemifield on the magnitude and lateralization of pre-stimulus alpha oscillations, and the P1 and N1. We reasoned, first of all, that if top-down inhibition is dependent on the need to resolve competition for limited processing resources, in a context in which the assignment of relevance to visual hemifield is fixed, top-down inhibition might no longer be necessary. This would be reflected in the absence of a modulation of pre-stimulus alpha asymmetry - just like other sensory (e.g., auditory) brain regions do not show active suppression by alpha-band oscillatory activity in attention studies that only employ visual stimuli. Moreover, if the P1 reflects the same functionality as alpha does, as some researchers propose (Klimesch, 2011), namely top-down inhibition, the ipsilateral P1 attention effect should also disappear. Lastly, if the N1 attention effect reflects facilitation of relevant stimulus processing, this effect should remain present, and possible be more pronounced over contralateral posterior brain regions that process information from the relevant hemifield.

To test our predictions, we ran three EEG experiments. In Experiment 1, participants sustained attention to a location in the left hemifield for 80 minutes and had to press a button upon detection of a rare target stimulus. In Experiment 2, participants viewed the same stimuli as in Experiment 1, but now under passive viewing conditions, to determine to what extent effects observed in Experiment 1 could be attributed to attention or the specific stimuli used. Experiment 3 concerned a replication of Experiment 1, but with different visual stimuli. Moreover, in Experiment 3, half of participants sustained attended to the left, and the other half of participants sustained attended to the right, so that effects could be attributed to the direction of attention with greater confidence. To foreshadow our results, when the assignment of relevance to location was fixed, we observed no modulation of pre-stimulus alpha-band oscillatory activity, an ipsilateral P1 attention effect, and a bilateral N1 attention effect. These findings indicate that these well-known neural indices of attention reflect qualitatively different aspects of attention.

Experiment 1

Materials and Methods

Subjects. Thirty subjects were recruited from the University of Amsterdam student population. Nine participants were excluded from further analysis due to a malfunctioning common mode sense active electrode (5 participants), problems keeping fixation (1 participant), an inability to perform the task correctly due to a lack of sleep the previous night (1 participant; experiment was aborted), or general poor data quality (2 participants). All data presented here, including behavioral data, are from the remaining 21 participants (11 female; mean age: 21.6, SD: 2.3). All participants had normal or corrected-to-normal vision, no history of mental or neurological disorders and were excluded from participation if they reported getting more than two hours less sleep than usual the night prior to the experiment. The study was approved by the ethical committee of the University of Amsterdam. All participants gave their informed consent and were paid € 7,- per hour.

Stimuli and Procedure. A modified version of the sustained attention paradigm employed by (MacLean et al., 2009) (Exp 1, stable version) was used. In this task, participants are required to visually discriminate briefly presented rare target stimuli (short lines) from standard non-targets (long lines) (see Figure 1, left panel), by pressing a button upon target detection. Responses are to be withheld for non-targets.

Participants sat at a viewing distance of 110 cm in front of a 17-inch BenQ TFT monitor with a refresh rate of 60 Hz. They were instructed to maintain fixation on a central fixation dot (0.11° × 0.11°) at all times, and to covertly direct their attention continuously to a location 3° to the left and 1.5° down from fixation. At this location, a placeholder, composed of many short lines (0.03° × 0.12°), was positioned within a 0.21° × 2.44° space on a black background. Every 2 seconds, a light gray line was briefly (150ms) presented at the to-be-attended location, followed directly by the placeholder, which thus also served as a masking stimulus (see Figure 1). This line was either of standard length (non-target) or, in 20% of trials, slightly shorter (target stimulus) (see below). Thus, participants had to continuously direct their attention to one hemifield. The other hemifield was never relevant. Stimuli were only ever presented at the attended location. Since it is possible that attention waxed and waned during the task, the terms sustained and continuous attention are used to denote that only one location was ever relevant during the entire task.

Prior to the start of the main task, individual performance was calibrated for each participant using Parameter Estimation by Sequential Testing (PEST) (Taylor and Creelman, 1967) (MacLean et al., 2009). PEST is a thresholding procedure that adaptively changes the step size between testing levels to estimate the desired level of an independent variable. In the present study, the procedure adjusted the length of the short line until a stable performance of 80% accuracy (i.e., the target is detected in 80% of trials) was reached. The only difference between the PEST procedure and the main task was a higher target to non-target ratio (1:3.5 vs. 1:5).

Long lines were always 1.89° in length. Short-line length varied across subjects between 1.21-1.59° (mean 1.40°, SD: 0.10°). Line width (0.03°) was constant for both long and short lines. To prevent participants from assessing the line length of stimuli by comparison to the length of the lines comprising the placeholder, each placeholder element was vertically repositioned by a random amount (within -0.06° to +0.06°) upon each presentation.

Because PEST employs a dynamic stopping rule, the duration of the procedure varied modestly between participants (between 7 and 13 minutes). During the PEST procedure, participants were given auditory feedback indicating a hit, a miss or a false alarm. After completion of the PEST procedure, the main task was performed for 80 minutes. Each participant completed 2400 trials in total of which 480 were target trials.

Every 10 minutes, participants were prompted to rate both their motivation to perform well and their aversion towards the task on a seven-point scale (1: no aversion/motivation; 7: strong aversion/motivation). After performing the task for 60 minutes, a new screen was displayed informing participants of a chance to gain an additional sum of money – an option that was unknown to them up until then. This manipulation was designed to motivate participants to do their utmost best during the remainder of the task, so that in separate analyses (not reported here) we could study the effects of time-on-task and motivation on neural activity and attentional performance. Specifically, participants were told that they could receive € 30,- on top of their nominal compensation if they outperformed at least 65% of the other participants during the last 20 minutes of the task (Lorist et al., 2009).

Behavioral analyses. Our main index of behavioral performance was expressed as *A'*, a nonparametric measure of perceptual sensitivity from signal detection theory (Stanislaw & Todorov, 1999). *A'* is dependent on hits, misses, false alarms (FAs) and correct rejections (CRs), and is calculated as follows:

$$A' = .5 + \frac{(H - F)(1 + H - F)}{4H(1 - F)}$$

If $H \geq F$, where H is Hit rate [Hits / (Hits + Misses)] and F is false alarm rate [FAs / (FAs + CRs)]. A' can take any value between 0.5, meaning that target stimuli are indistinguishable from non-targets, and 1, signaling perfect performance.

EEG data acquisition and preprocessing. EEG data were DC recorded at 512 Hz using a BioSemi ActiveTwo 64 Ag-AgCl channel setup (BioSemi, Amsterdam, The Netherlands) placed according to the international 10-10 system. The EEG signal was pre-amplified at the electrode to improve the signal-to-noise ratio with a gain of 16, and digitized at 24-bit resolution with a sampling rate of 512 Hz. Each active electrode was measured on-line with respect to a common mode sense active electrode producing a monopolar (nondifferential) channel. Four external electrodes recorded the electro-oculogram from vertical (below and above the left eye) and horizontal (next to the left and right outer canthi) ocular sites. Two additional electrodes were placed on both earlobes.

Preprocessing was done using the EEGLAB toolbox (Delorme and Makeig, 2004) operating in the MATLAB (Mathworks, Natick, MA) environment. The continuous EEG data were first high-pass filtered offline at 0.1 Hz and subsequently segmented into epochs from -2000 ms to +2000 ms peri-stimulus, of which 1-second buffer zones on each end were meant to accommodate the edge artifacts that may result from wavelet convolution (see below). All trials were then visually inspected; those containing large artifacts due to electromyographic (EMG) activity or with horizontal eye movements were removed. Bad channels were also removed and reinterpolated using spline interpolation. Independent component analysis was performed next (EEGLAB's runica algorithm). If a component capturing residual horizontal eye movement activity was present, the activity of this component was used to remove remaining trials with horizontal eye movements. Components containing eye blink or other artifacts clearly distinguishable from genuine neural activity were subtracted from the data. Finally, epochs were average referenced and separated into different conditions according to trial-type (hit, miss and CR) and used in subsequent time-frequency and ERP analyses. FA trials were too few to include in the analyses.

Time-frequency decomposition. Time-frequency representations of the EEG data were obtained using custom scripts written in MATLAB. Hit and miss epoch counts were first equalized per participant, such that the same number of hit and miss trials (mean: 152 trials, SD: 30, range 92-213) were used in analyses examining the effects of spatial attention on oscillatory dynamics. For each condition separately, all epochs were concatenated into one long time series and subsequently convolved with a family of complex Morlet wavelets

(Cohen, 2014). These wavelets consist of a complex exponential tapered with a Gaussian window:

$$e^{i2\pi ft} \cdot e^{\frac{-t^2}{2s^2}}$$

where f is frequency, t is time, and s represents the width of the Gaussian. Frequency increased from 2 to 80 Hz in 30 logarithmically spaced steps. s equals $x/2\pi f$, where x increased logarithmically from 3 to 12 in the same number of steps. Following convolution, data were reshaped back into individual epochs. Concatenation and subsequent reshaping was performed primarily for computational efficiency and also to minimize edge artifacts. Edge artifacts were not removed but were instead confined to 1s long buffer zones at both extremes of each epoch. From this time-frequency representation of the data, we computed trial-averaged power values.

To examine effects of continuous attention to one hemisphere on pre-stimulus alpha activity over posterior scalp regions, raw alpha power values (8-14Hz; e.g., cf. (Kelly et al., 2006; Sauseng et al., 2005; Thut et al., 2006; Worden et al., 2000) were averaged over the -1000 to -100ms pre-stimulus interval (cf. (Thut et al., 2006), separately for correct rejection, hit and miss trials and lateral posterior scalp regions where alpha power was most pronounced. Specifically, pre-stimulus alpha power was averaged over three electrodes over ipsilateral posterior occipital cortex (POC) (electrodes P07, P5 and P7) and three electrodes over contralateral POC (electrodes PO8, P6, P8). Then, for each subject and condition separately, we calculated a lateralization index (Händel et al., 2011; Thut et al., 2006):

$$\frac{\alpha_{contralateral\ POC} - \alpha_{ipsilatral\ POC}}{\alpha_{contralateral\ POC} + \alpha_{ipsilateral\ POC}}$$

in which raw alpha power in each hemisphere is expressed relative to the total alpha power at both sites. This number is positive when $\alpha_{contralateral\ POC} > \alpha_{ipsilateral\ POC}$ and negative when the inverse is the case. To determine if alpha power lateralization was modulated by attention, a paired t test was done to determine if alpha lateralization differed between trials in which the target stimulus was detected vs. missed.

ERP analyses. We next examined the effects of continuous attention to one hemifield on early stimulus processing, as indexed by the P1 and N1 components. Epochs were low-pass filtered (30Hz) using EEGLAB's basic FIR filter, baselined to -200 to 0ms pre-stimulus, and averaged separately for hit, miss and correct rejection trials. Consistent with previous ERP studies, the condition-average P1 and N1 were most pronounced over lateral posterior scalp regions (see Results). Interestingly, these regions were identical to those over which

pre-stimulus alpha power was most pronounced. We thus confined our analyses to the ERPs at the same two electrode pools (ipsilateral POC; average of P07, P5 and P7 and contralateral POC; average of PO8, P6, P8). For each subject, we obtained the mean voltage value over a 35-ms time window centered around their P1 or N1 peak latency. P1 peak latency was defined as the largest positive deflection occurring within 110-180 ms post-stimulus, while N1 peak latency was defined as the largest negative deflection occurring within 190-260ms post-stimulus. These larger time windows were based on the group-average P1 and N1 latencies averaged across conditions and consistent with previous studies. The P1 and N1 amplitude of the participants were entered as dependent measures in separate repeated measures ANOVAs with the within-subject factors Condition (hit, miss) and Hemisphere (ipsilateral POC, contralateral POC). In case of a significant interaction between Condition and Hemisphere, *t* tests were run for each hemisphere separately, to determine whether effects of attention were confined to one hemisphere or present in both hemispheres.

Results

Behavior. Participants were well capable of discriminating target from non-target stimuli, as indicated by an average A' of .87 (SD: +/- .03; range .82 to .92). Average reaction time was 692ms.

Effects of continuous attention on pre-stimulus alpha-band oscillatory activity. As mentioned in the introduction, previous probabilistic cueing studies have shown enhanced pre-stimulus alpha power over posterior regions ipsilateral to the attended location, thought to protect against input from irrelevant or distracting input, and/or reduced pre-stimulus alpha power (or release of inhibition) over contralateral posterior regions, thought to facilitate future visual processing at the attended position (for recent reviews, see e.g., Jensen and Mazaheri, 2010; Klimesch, 2012). However, as can be seen in Figure 2, in the current study, when hemifield relevance was fixed across the entire experiment, we observed relatively lower alpha power over irrelevant (ipsilateral) vs. relevant (contralateral) posterior scalp regions (CRs: t(20 = 1.84, p = 0.081; Hits: t(20) = 1.545, p = 0.138; Misses: t(20) = 2.239, p = 0.037). This "flipped" alpha asymmetry is visualized for correct rejection trials in Figure 2A, which shows unbaselined alpha power separately for ipsi- and contralateral POC, and in Figure 2B, which displays the scalp topography of the difference in alpha power in the pre-stimulus interval between contra- vs. ipsilateral POC, normalized by total alpha power at both hemispheres (i.e., the alpha lateralization index). Thus, in contrast to previous studies, we

observed relatively lower alpha power over irrelevant vs. relevant visual scalp regions. This finding may provide support for recent proposals that alpha activity indexes an active, top-down inhibitory control process that is only called upon when irrelevant visual brain areas actively compete with relevant visual brain areas for limited attentional resources.

The fact that there was pre-stimulus alpha power over relevant visual areas fits with recent studies showing a parabolic relationship between pre-stimulus alpha and attention, with intermediate levels of alpha activity over sensory cortex predicting optimal stimulus processing (Linkenkaer-Hansen et al., 2004; Rajagovindan and Ding, 2011; Zhang and Ding, 2010). Indeed, the flipped asymmetry in pre-stimulus alpha oscillatory activity was significantly pronounced in miss compared to hit trials ($t(20) = -2.63$, $p = 0.016$). This latter finding concurs with previous work indicating that too high alpha activity over relevant visual regions may actually impair performance (Bengson et al., 2012; van Dijk et al., 2008). Post-hoc analyses showed that the difference in pre-stimulus alpha activity between hit and miss trials (normalized by their sum) is only significant over contralateral (right hemisphere) scalp regions ($t(20) = -2.920$, $p = 0.008$), not over ipsilateral (left hemischere) scalp regions ($t(20) = -1.720$, $p = 0.101$).

Previous studies have reported that with time on task, there is a shift in the distribution of attention toward the right hemifield, which is also reflected in the pattern of alpha power over posterior brain regions. Specifically, a recent EEG study in which participants attended to peripheral stimuli and also monitored stimuli at fixation, found that pre-target alpha activity became more prominent over the right, relative to left, hemisphere, as the task progressed over 48 minutes (Newman et al., 2013). One could thus argue that the greater alpha power observed over right (contralateral) vs. left (ipsilateral) scalp regions simply reflects this time on task effect. Yet, as can be seen in Figure 2C, the observed "flipped" lateralization was already present during the first 5 minutes of the task, arguing against an interpretation simply in terms of time on task.

Effects of continuous attention on early stimulus processing: ERPs. In previous EEG studies of spatial attention, participants typically switched between attending left and attending right either on a trial-by-trial or block-by-block basis. These studies consistently observed *bilateral* P1 and N1 components, which were modulated in amplitude by attention (e.g., Luck, 1995; Hillyard and Anllo-Vento, 1998). Although these modulations of early sensory processing were typically larger and visible first over contralateral compared to ipsilateral posterior scalp regions in many studies, to our knowledge, in most studies they were observed over, and/or localized to, visual regions in both hemispheres. Yet, in the

present study, as can be seen in Figure 3A, continuous attention to one hemifield was associated with *completely lateralized* P1 and N1 components. Specifically, in line with the idea that the P1 reflects inhibition, and the N1 facilitation of stimulus processing, a P1 could only be observed over irrelevant (ipsilateral) visual regions (main effect of Hemisphere; $F(1,20)=13.98$, $p=.001$), whereas an N1 was only visible over relevant (contralateral) visual regions (main effect of Hemisphere; $F(1,20)=18.73$; $p<.001$). Thus, notably, even though a stimulus was only presented at the attended location, i.e., no stimulus was presented at the unattended location, a clear event-related P1 was observed only over visual regions representing the unattended location, not over visual regions representing the attended location.

Of further note, as shown in Figure 3A and 3B, the amplitude of the P1 was modulated by attention only over ipsilateral posterior scalp regions, as reflected in a significantly larger P1 in hit vs. miss trials (significant interaction between Condition and Hemisphere; $F(1,20)=8.95$, $p=.007$), but not over contralateral scalp regions (main effect of Condition was only significant at ipsilateral sites: $t(1,20)=3.34$, $p=.003$, not at contralateral sites: $t(1,20)=-0.71$, $p=.484$). In contrast, the amplitude of the N1 was significantly larger only over contralateral posterior electrodes in hit vs. miss trials (significant interaction between Condition and Hemisphere; $F(1,20)=11.0$, $p=.003$), but not over ipsilateral scalp regions (main effect of Condition was only significant at contralateral sites: $t(1,20)=-5.23$, $p<.001$, not at ipsilateral sites: $t(1,20)=-0.67$, $p=.513$). A Bayes Factor analysis (Rouder et al., 2009) indicated that the null hypothesis (no difference between Hit and Miss trials) was 3.51 times more likely to be true than the alternative hypothesis (a difference between conditions) for the contralateral P1; this ratio was 3.59 for the ipsilateral N1. Thus, both absolute P1 and N1 amplitudes and their attentional modulation were perfectly lateralized to irrelevant and relevant visual regions, respectively. These findings provide strong support for the idea that the P1 reflects an inhibitory process, and the N1 attentional facilitation. It should also be noted that, like the observed flipped alpha asymmetry, the P1 and N1 components already showed strong lateralization to ipsi- and contralateral POC sites, respectively within the first 5 minutes of the task (see Figure 3C). This indicates that the above reported effects of spatial attention were already present right from the start, and likely unrelated to having to do a task for prolonged period of time.

Experiment 2

The complete lateralization of the absolute P1 and N1 components observed in Experiment 1 is somewhat surprising given that visual stimuli are widely thought to trigger bilateral activation of visual cortex, reflected in bilateral occurrence of these exogenous ERPs at the scalp level. We therefore ran a second experiment. 8 participants (4 female; mean age: 21.4, SD: 3.1) *passively* viewed the same line stimuli as in Experiment 1, which randomly appeared in the left or right hemifield with equal probability every two seconds, while they maintained central fixation. Thus, in contrast to Experiment 1, in this second experiment, attention was not directed to one hemifield, but stimuli were passively viewed, and there was visual input from both hemifields. As subjects performed no task, target length was similar for all subjects and defined as the average target length used in Experiment 1 across subjects. Of further note, as in Experiment 1, placeholders were shown, but now on both the left and the corresponding right location.

ERP analyses revealed that under passive viewing conditions, as expected, the N1 to stimuli presented on the left became bilateral (see Figure 4): An N1 was observed over both contralateral and ipsilateral posterior scalp regions, although its amplitude was relatively small, conceivably due to the fact that subjects were passively viewing the stimuli. The N1 first peaked over contralateral scalp regions (209 (+/- 23) ms) and then over ipsilateral ones (262 (+/- 12) ms). However, and admittedly to our surprise, the P1 to stimuli presented on the left remained completely lateralized to ipsilateral scalp regions under passive viewing conditions with bilateral input. The same pattern was observed for stimuli presented on the right; they too elicited an ipsilateral P1 (which now peaked over right POC), and a bilateral N1. This pattern of findings was confirmed statistically by repeated measurements ANOVAs with P1/N1 amplitude as the dependent measure (cf. Experiment 1) and Hemisphere (left POC (lPOC), right POC (rPOC)), and Stimulus Location (left, right) as within-subject factors. Specifically, for the P1, a significant interaction between Hemisphere and Stimulus Location was observed ($F(1,7)=8.8$, $p=0.021$), reflecting the fact that a P1 to left stimuli was observed over lPOC, while a P1 to right stimuli was observed over rPOC. Yet, this interaction was far from significant for the N1 ($F(1,7)=.073$, $p=.80$), confirming its bilateral distribution under passive viewing conditions. These findings suggest that the P1 lateralization observed in Experiment 1 cannot be (solely) due to continuous attention to one hemifield, but may reflect specific aspects of our stimulus or task design. For example, the P1 response in contralateral regions may have simply been too weak to be measured at the scalp due to our low luminance, isoluminant stimuli.

Experiment 3

In Experiment 1, continuous attention to the left was associated with completely lateralized P1 and N1 components and attentional modulations. Yet, in Experiment 2, we found that under passive viewing conditions, while the N1 became bilateral, the P1 remained completely lateralized to ipsilateral scalp regions, rendering interpretation of the P1 findings in Experiment 1 difficult. We therefore conducted a follow-up experiment, in which, again, participants had to attend to one hemifield during the entire experiment and stimuli were only ever presented at the to-be-attended location. Critically, however, this time non-masked, brighter, and bigger visual stimuli were used which elicited both a bilateral P1 and a bilateral N1, as well as bilateral P1 and N1 attentional modulations, in a traditional attentional cueing task (Sauseng et al., 2005). We were specifically interested to see if with these different stimuli, we would replicate the lateralizations of the P1 and N1 attention effects observed in Experiment 1, which one would predict if these were in fact caused by the specific task of continuously attending to one hemifield. In addition, the isoluminant attention placeholder and mask was removed to ensure strong visual responses, as well as to exclude the possibility that the observed pre-stimulus alpha pattern in Experiment 1 was related to the continuous presence of this non-relevant stimulus at the attended location. Of further importance, half of subjects attended to the left and stimuli were only presented on the left, while the other half of subjects attended to the right and stimuli were only presented on the right. Pre-stimulus alpha activity has been shown to be greater in general over right compared to left posterior brain regions, i.e., during resting conditions (Wieneke et al., 1980). Since in Experiment 1, participants were always attending left, but never right, it is possible that the observed relatively greater alpha over contralateral (right) vs. ipsilateral (left) scalp regions thus simply reflects a baseline effect. The inclusion of a condition in which participants are continuously attending to a right location allowed us to investigate this. If the observed flip in alpha lateralization in Experiment 1 simply reflects a baseline difference in alpha activity between the right and the left hemisphere, one would predict the pattern of alpha lateralization to be identical in the attend-left and attend-right conditions (i.e., greater alpha over right vs. left posterior regions). However, if it is related to continuous attention to one hemifield, one would expect the attend-right condition to also be associated with greater alpha activity over contralateral (but now left) vs. ipsilateral (but now right) posterior sites. Thus, Experiment 3

aimed to replicate the attention effects reported in Experiment 1 with different stimuli, and to extend these findings by including an attend-right condition.

Materials and Methods

Subjects. Thirty subjects (25 female; mean age: 21.5, SD: 2.5) were recruited from the University of Amsterdam student population. All participants had normal or corrected-to-normal vision, and no history of mental or neurological disorders. The study was approved by the local ethical committee. All participants gave their informed consent and were paid € 10,- per hour or participated for research credit.

Stimuli and Procedure. The task and procedure were similar to Experiment 1, except for the following changes. First, as can be seen in Figure 1 (right panel), stimuli were (i) slightly bigger (1° (width) × 2° (height); cf. (Sauseng et al., 2005)), (ii) presented more lateral (5°), more in line with previous studies of spatial attention, and (iii) appeared on average every 1.9 seconds (SOA jittered between 1800 and 2000ms) for 50ms. Second, the placeholder was removed. Third, half of the subjects continuously attended to the left and stimuli only occurred on the left, whereas the other half of subjects continuously attended to the right and stimuli only occurred on the right. Fourth, the main task lasted 40 minutes (vs. 80 min in Experiment 1). Thus, each participant completed 1200 trials in total of which 240 were target trials.

Behavioral analyses. Our main index of behavioral performance was again expressed as *A'*, a nonparametric measure of perceptual sensitivity from signal detection theory (Stanislaw & Todorov, 1999).

EEG data acquisition, preprocessing, and analyses. EEG data acquisition, preprocessing and time-frequency and ERP analyses were identical to those in Experiment 1 (see above). Only the electrode selection was different for the N1 analyses, as inspection of the data revealed that the N1 now peaked over electrode sites P03/4, P3/4, P5/6, reflecting the more lateral presentation of the stimuli in Experiment 3. In addition, conceivably due to the higher luminance of the stimuli and the fact that they were no longer presented on top of isoluminant placeholders (Grent-'t-Jong et al., 2011; Johannes et al., 1995; Wijers et al., 1997), the P1 and N1 components peaked earlier in Experiment 3 than in Experiment 1, and the following time windows were used for peak picking: 80-140ms (contralateral P1), 100-160ms (ipsilateral P1), 140-200ms (contralateral N1) and 160-220 (ipsilateral N1). Lastly, in all statistical

analyses, Attention Condition (attend-left, attend-right) was added as an additional, between-subjects factor.

Results

Behavior. Participants were again well capable of discriminating target from non-target stimuli, as indicated by an average A' of 0.88 (SD: +/- .04) in the attend-left group and of 0.88 (+/- .05) in the attend-right group. Average reaction time was 602 ms (SD: 53ms) in the attend-left group, an 605 ms (SD: 97ms) in the attend-right group. Groups did not differ in their task performance (A': $t(28)=-.59$, $p=.56$; reaction time: $t(28)=-.11$, $p=.91$).

Effects of continuous attention on pre-stimulus alpha-band oscillatory activity. In Experiment 1, continuous attention to the left was associated with relatively greater alpha power over right (contralateral) vs. left (ipsilateral) scalp regions. This 'flip' in alpha lateralization was replicated in the follow-up experiment in the attend-left condition (see Fig. 5, left panel). The critical question was, however, whether this pattern of alpha lateralization reflects our attention manipulation, or simply reflects a baseline difference in alpha activity between the right and left hemisphere. In line with a baseline effect (Wieneke et al., 1980), the same alpha lateralization was observed in the attend-right condition: here too, pre-stimulus alpha activity was larger over right compared to left posterior scalp regions (Fig. 5, right panel). Greater alpha power over right compared to left POC (normalized by total alpha power at both hemispheres) in both the attend-left and attend-right groups was confirmed statistically by a significant main effect of Hemisphere ($F(1,28)=4.78$, $p=.037$) and the absence of a significant interaction between Hemisphere and Attention Condition ($F(1,28)=.084$, $p=.77$). Thus, importantly, even though we used a task that differed in several aspects from the one used in Experiment 1 (e.g., no masks), in Experiment 3, we replicated the pattern of alpha asymmetry observed in Experiment 1 (i.e., more alpha over right vs. left POC), but extended this finding by showing that is likely reflects a pattern of resting alpha asymmetry. Although in Experiment 1, significantly higher alpha power over relevant vs. irrelevant visual areas was observed in trials in which the target went undetected compared to when it was seen, this relationship was not observed in Experiment 3 (main effect Condition: $F(1,28)=.45$,$p=.51$; interaction Condition and Attention Condition: $F(1,28)=1.5$, $p=.23$). A Bayes Factor analysis (Rouder et al., 2009) indicated that the null hypothesis (no difference between Hit and Miss

trials) was 4.2 times more likely to be true than the alternative hypothesis (a difference between conditions).

Effects of continuous attention on early stimulus processing: ERPs. In Experiment 1, continuous attention to one hemifield was associated with completely lateralized P1 and N1 components to ipsilateral and contralateral scalp regions respectively. In particular, the absence of a contralateral P1 was rather surprising in light of the fact that this component is commonly assumed to reflect stimulus-evoked visual processing. As can be seen in Figure 6, in Experiment 3, with stronger visual input, a clear bilateral P1 was observed. This observation is in line with the common notion that the P1 reflects visual activity triggered by visual events, and together with the results from Experiment 2, indicates that the completely lateralized P1 in Experiment 1 likely reflects specific aspects of the particular stimuli (e.g., low contrast) used. The critical question is, however, if we would replicate the ipsilateral P1 attention effect in Experiment 3. Strikingly, although the early P1 response now occurred over both hemispheres, in both the attend-left and the attend-right condition, its modulation by continuous spatial attention was still strongly asymmetric (Figure 6A). That is, the amplitude of the P1 was significantly larger only over ipsilateral posterior scalp regions in hit vs. miss trials, but not over contralateral scalp regions (significant interaction between Condition and Hemisphere: $F(1,28)=7.1$, $p=.013$; main effect of Condition was only significant at ipsilateral sites: $t(29)=2.8$, $p=.008$; not at contralateral sites: $t(29)=-.27$, $p=.79$). This was the case in both the attend-left and the attend-right condition (interaction between Hemisphere, Condition, and Attention Condition was not significant: $F(1,28)=2.9$, $p=0.10$). A Bayes Factor analysis (Rouder et al., 2009) indicated that the null hypothesis (no difference between Hit and Miss trials) was 4.97 times more likely to be true than the alternative hypothesis (a difference between conditions) for the contralateral P1. Thus, in Experiment 3, replicating Experiment 1, continuous attention to one hemifield was again associated with an ipsilateral modulation of the P1.

As for the N1, in Experiment 1 the N1 was only observed contralaterally under continuous attention conditions, while Experiment 2 showed a clear bilateral N1 under passive viewing conditions. In Experiment 3, an N1 was again clearly visible over contralateral scalp regions, while over ipsilateral sites, a negative-going deflection in the N1 time window barely peaked below the zero-line (Figure 6B; main effect of Hemisphere: $F(1,28)=19.5$, $p<.001$). Nevertheless, in the N1 time window, an attentional modulation was now observed over both ipsilateral and contralateral scalp regions. This was confirmed by statistical analyses which showed significantly greater negativity in hit compared to miss

trials over not only contralateral, but also ipsilateral, posterior electrodes (significant main effect of Condition; $F(1,28)=13.4$, $p=.001$; the interaction between Condition and Hemisphere was not significant: $F(1,28)=0.68$, $p=.42$; neither was the interaction between Condition, Hemisphere, and Attention Condition: $F(1,28)=0.41$, $p=.53$).

Thus, in Experiment 3, we replicated two main findings of Experiment 1; the consistent assignment of relevance to one hemifield was associated with greater alpha activity over right compared to left posterior regions regardless of the direction of attention (i.e., no modulation of pre-stimulus alpha activity) and an ipsilateral P1 attention effect. With the higher contrast stimuli, however, a bilateral N1 attention effect was observed.

General Discussion

The aim of the series of EEG studies reported here was to gain a better understanding of the functional role of pre-stimulus alpha oscillations, the P1, and the N1 in selective attention. To this end, participants continuously attended to one and the same hemifield during the entire experiment, and stimuli were only presented at the attended location. We reasoned that when location relevance was fixed to one hemifield, this would allow us to better separate inhibitory and facilitatory effects of attention. There were two main findings. First, in contrast to previous studies in which subjects always alternated between attending left and right, in two experiments with a slightly different task design and different stimuli (Experiments 1 and 3), the consistent assignment of relevance to one hemifield was characterized by the absence of the typically observed attention-related lateralization in pre-stimulus alpha activity (e.g., Thut et al., 2006; Worden et al., 2000). Second, again in striking contrast to previous studies in which subjects alternated between attending left and right and which typically observed bilateral attentional modulations of early sensory processing, in both experiments, we found a P1 attention effect exclusive to ipsilateral (i.e., irrelevant) posterior scalp regions. Yet, the N1 attention effect remained bilateral, although only in the case of strong visual input in Experiment 3. With the weaker visual stimuli in Experiment 1, the N1 attention effect was only observed over contralateral posterior regions. These observations substantiate the idea that the P1 and N1 effects reflect qualitatively different aspects of attention, and corroborate previous findings indicating that the P1 reflects an inhibitory process, and the N1 attentional facilitation (Couperus and Mangun, 2010; Freunberger et al., 2008; Klimesch, 2011; Luck, 1995; Luck et al., 1994; Talsma et al., 2007, 2005). As discussed in more detail below,

together, these findings suggest a functional dissociation between pre-stimulus alpha activity, the P1 and the N1 component, and have important implications for cognitive neuroscience models of attention.

No spatial attention-related pre-stimulus alpha lateralization

To our knowledge, in every previous study of spatial attention so far, the direction of alpha asymmetry was always such that more alpha power was observed over irrelevant compared to relevant brain regions. In contrast, here, in two experiments, when attention was sustained to one hemifield, a "resting" pattern of alpha lateralization was observed (Wieneke et al., 1980), with pre-stimulus alpha power being higher over right compared to left posterior scalp regions regardless of the direction of attention (left or right). The relative absence of alpha power over irrelevant regions is in line with recent proposals that alpha power reflects a top-down inhibitory control process, only required when irrelevant regions actively compete with relevant regions for limited attentional resources (Jensen and Mazaheri, 2010; Klimesch, 2012). This is conceivably less likely the case in conditions in which only one hemifield is ever relevant and stimulated. Just like other sensory (e.g., auditory) regions do not display active suppression by alpha oscillatory activity in attention studies employing only visual stimuli, the non-involved visual hemisphere does not require active suppression by alpha oscillations in the current study. Future work is necessary to determine the mechanisms that control the modulation of alpha activity, although both neocortical and thalamic pathways are likely implicated (Jensen et al., 2014).

In Experiment 1, we observed relative greater alpha power over right compared to left posterior regions in Miss compared to Hit trials. This finding was not replicated in Experiment 3. It is possible that differences in the duration of the task – 80min in Experiment 1 and 40min in Experiment 2 – can explain this discrepancy in findings. A previous study found that pre-target alpha activity became more prominent over the right, relative to left, hemisphere, while subjects did an attention task over a period of 48 minutes (Newman et al., 2013). Yet, it should be noted that the observed pre-stimulus alpha lateralization was already present during the first 5 minutes of the task.

An ipsilateral P1 modulation and a bilateral N1 modulation

In two experiments, we furthermore found that continuous attention to one hemifield selectively modulated the amplitude of the ipsilateral P1. The presence of an ipsilateral P1 attention effect combined with the absence of this effect contralaterally is not easily

reconciled with the sensory gain model of attention (Hillyard et al., 1998), which interprets the P1 attention effect as reduced visual processing of unattended stimuli and would certainly predict a contralateral P1 attention effect (Luck, 1995). Our findings also have implications for the inhibition-timing account of the P1 by Klimesch (2011), which - based on the notion that the P1 is generated and modulated at least in part by alpha oscillations - proposes that the P1 reflects the same type of functionality as alpha does and reflects inhibitory processes that have different functions in task relevant and irrelevant neural structures. Specifically, in this account, a large P1 over ipsilateral regions reflects top-down suppression of item processing, while the larger P1 to attended versus unattended items at contralateral regions indexes more effective item processing due to an inhibition-modulated increase in signal to noise ratio. While our data support a primary role for the P1 in blocking sensory processing in irrelevant regions, they importantly indicate a functional dissociation between pre-stimulus alpha and the P1; Whereas the inhibitory process reflected by pre-stimulus alpha activity over irrelevant regions disappeared in our specific situation in which the irrelevant hemifield was never relevant, the inhibitory process reflected by the ipsilateral P1 attention effect remained present. Therefore, while pre-stimulus alpha activity may reflect active, top-down inhibition required to protect against visual input from task-irrelevant positions, the ipsilateral P1 effect in contrast may reflect stimulus-triggered inhibition of processing in the irrelevant hemisphere that is not or at least much less dependent on competition for limited processing resources. Blocking of information processing in irrelevant networks may direct the flow of information processing to those brain regions that represent information that is relevant for encoding (Klimesch, 2011).

In particular, the P1 effect may reflect a competitive mechanism of a more local nature, such as inter-hemispheric inhibition (Kinsbourne, 1977). It is noteworthy in this respect that fMRI and microelectrode work in monkeys has shown that the ipsilateral primary somatosensory cortex is inhibited by sensory stimulation (Lipton et al., 2006). In humans, unilateral touch of fingers has also been associated with transient deactivation of the ipsilateral primary somatosensory cortex, in addition to the well-known activation of the contralateral primary somatosensory cortex (Hlushchuk and Hari, 2006). The ipsilateral deactivation is thought to result from transcallosal inhibition. At the level of visual cortex, there is also evidence that initial activation in ventral stream areas is provided by dorsal stream structures rather than input along the ventral stream through V1 and V2 (Chen et al., 2007; Schroeder et al., 1998). Early ventral stream processing can moreover be modulated by feedback-activity from prefrontal regions (Fuster et al., 1985). The existence of such

nonfeedforward routes is in line with an interpretation of the P1 in terms of a stimulus-triggered modulation of early feedforward visual processing. It is noteworthy in this respect that the P1 not only includes contributions from extrastriate areas (Foxe and Simpson, 2002; Mangun et al., 1997; Woldorff et al., 1997), but may also reflect delayed re-entrant feedback to V1 (Noesselt et al., 2002). Whether the ipsilateral P1 modulation observed in the current study is instantiated via transcallosal connections or feedback from higher brain regions requires additional research.

It should be noted that in the current study, attentional effects were quantified by comparing neural activity in hit versus miss trials, whereas in traditional designs, the comparison is typically between neural responses to attended versus unattended stimuli. One may argue that this may have affected our ability to observe a contralateral P1 attention effect, as in principle, in both hit and miss trials, participants should have been attending to the same location. Miss trials may have resulted from lapses in attention, leading to reduced visual processing, which may be different in nature from effects on visual processing of attention being directed to another location in space. However, a lapse of attention should also result in reduced visual processing contralaterally. The fact that we did not observe a contralateral P1 attention effect critically argues against the idea that failures to detect the target stimulus could have simply resulted from reduced visual processing per se.

In contrast to the P1 effect, the N1 attention effect was observed bilaterally, and over occipital-temporal regions, replicating previous studies. The occipital-temporal N1 has been associated with a stimulus discrimination process (Hopf et al., 2002; Ritter et al., 1982; Vogel and Luck, 2000). Attention may thus have facilitated target discrimination processes in the ventral stream of both hemispheres.

Task context

Together, our findings indicate that the brain does not distribute attention simply based on the current task instruction (e.g., ‘attend left’), but takes previous visual input, trial history and/or overall trial type probability (or global task context) into account as well – a view consistent with previous attention studies (Eimer, 1996; Luck et al., 1990; Slagter et al., 2006, 2005; Vossel et al., 2006). This raises important questions regarding the extent to which neural and behavioral effects that have traditionally been attributed to attention, such as in probabilistic cueing paradigms, were confounded by perceptual expectations. Indeed, a growing body of research shows that expectations can modulate early sensory processing (Kok et al., 2012; Rauss et al., 2011; Summerfield and Egner, 2009), in line with conceptualizations of visual

cortex activity in terms of predictive coding, where neural signals are regarded less related to a stimulus per se, but a consequence of predictive coding mechanisms, calculated on the basis of previous input to the visual system (Barlow, 1985; Mumford, 1992). In our experiment, attention and expectation toward a target stimulus always coincided, and both processes therefore likely contributed to observed effects. Future studies are necessary to disentangle effects of attention and prediction on early stimulus processing.

Conclusions

In conclusion, our data demonstrate a functional dissociation between pre-stimulus alpha activity, the P1, and the N1. That is, while pre-stimulus alpha-band activity may reflect a top-down inhibitory mechanism that critically depends on functional competition between relevant and irrelevant sensory regions, the early P1 attention effect likely reflects a stimulus-triggered blocking of sensory processing in irrelevant networks (bottom-up inhibition), and the N1 attention effect facilitation of processing of task-relevant information. Together, these findings shed further light on how attentional inhibition and facilitation are implemented in the brain. They also highlight the influence of overall task structure and top-down expectations on attentional control dynamics and stimulus processing.

Acknowledgements

We are very grateful to Rudy van den Brink for his help in programming the task, data collection and preprocessing, and to Mike X Cohen for advice about some of the spectral analyses. This work was supported by a Marie Curie reintegration grant to HAS and a VIDI grant from the Netherlands Organization for Scientific Research (NWO) to HAS.

References

Barlow, H.B., 1985. Cerebral cortex as a model builder., in: Models of the Visual Cortex. Wiley, Chichester, pp. 37–46.

Bengson, J.J., Mangun, G.R., Mazaheri, A., 2012. The neural markers of an imminent failure of response inhibition. Neuroimage 59, 1534–1539. doi:10.1016/j.neuroimage.2011.08.034

Chen, C.-M., Lakatos, P., Shah, A.S., Mehta, A.D., Givre, S.J., Javitt, D.C., Schroeder, C.E., 2007. Functional anatomy and interaction of fast and slow visual pathways in macaque monkeys. Cereb. Cortex 17, 1561–1569. doi:10.1093/cercor/bhl067

Cohen, M.X., 2014. Analyzing Neural Time Series Data: Theory and Practice. The MIT Press.

Couperus, J.W., Mangun, G.R., 2010. Signal enhancement and suppression during visual-spatial selective attention. Brain Res. 1359, 155–177. doi:10.1016/j.brainres.2010.08.076

Delorme, A., Makeig, S., 2004. EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. J. Neurosci. Methods 134, 9–21. doi:10.1016/j.jneumeth.2003.10.009

Eason, R.G., Harter, M.R., White, C.T., 1969. Effects of attention and arousal on visually evoked cortical potentials and reaction time in man. Physiology & Behavior 4, 283–289. doi:10.1016/0031-9384(69)90176-0

Eimer, M., 1996. ERP modulations indicate the selective processing of visual stimuli as a result of transient and sustained spatial attention. Psychophysiology 33, 13–21.

Foxe, J.J., Simpson, G.V., 2002. Flow of activation from V1 to frontal cortex in humans. A framework for defining "early" visual processing. Exp Brain Res 142, 139–150. doi:10.1007/s00221-001-0906-7

Freunberger, R., Höller, Y., Griesmayr, B., Gruber, W., Sauseng, P., Klimesch, W., 2008. Functional similarities between the P1 component and alpha oscillations. Eur. J. Neurosci. 27, 2330–2340. doi:10.1111/j.1460-9568.2008.06190.x

Fuster, J.M., Bauer, R.H., Jervey, J.P., 1985. Functional interactions between inferotemporal and prefrontal cortex in a cognitive task. Brain Res. 330, 299–307.

Grent-'t-Jong, T., Boehler, C.N., Kenemans, J.L., Woldorff, M.G., 2011. Differential Functional Roles of Slow-Wave and Oscillatory-Alpha Activity in Visual Sensory Cortex during Anticipatory Visual–Spatial Attention. Cereb. Cortex 21, 2204–2216. doi:10.1093/cercor/bhq279

Händel, B.F., Haarmeier, T., Jensen, O., 2011. Alpha oscillations correlate with the successful inhibition of unattended stimuli. J Cogn Neurosci 23, 2494–2502. doi:10.1162/jocn.2010.21557

Hillyard, S.A., Anllo-Vento, L., 1998. Event-related brain potentials in the study of visual selective attention. Proc. Natl. Acad. Sci. U.S.A. 95, 781–787.

Hillyard, S.A., Vogel, E.K., Luck, S.J., 1998. Sensory gain control (amplification) as a mechanism of selective attention: electrophysiological and neuroimaging evidence. Philos. Trans. R. Soc. Lond., B, Biol. Sci. 353, 1257–1270. doi:10.1098/rstb.1998.0281

Hlushchuk, Y., Hari, R., 2006. Transient Suppression of Ipsilateral Primary Somatosensory Cortex during Tactile Finger Stimulation. J. Neurosci. 26, 5819–5824. doi:10.1523/JNEUROSCI.5536-05.2006

Hopf, J.-M., Vogel, E., Woodman, G., Heinze, H.-J., Luck, S.J., 2002. Localizing visual discrimination processes in time and space. J. Neurophysiol. 88, 2088–2095.

Jensen, O., Mazaheri, A., 2010. Shaping functional architecture by oscillatory alpha activity: gating by inhibition. Front Hum Neurosci 4, 186. doi:10.3389/fnhum.2010.00186

Johannes, S., Münte, T.F., Heinze, H.J., Mangun, G.R., 1995. Luminance and spatial attention effects on early visual processing. Cognitive Brain Research 2, 189–205. doi:10.1016/0926-6410(95)90008-X

Kelly, S.P., Lalor, E.C., Reilly, R.B., Foxe, J.J., 2006. Increases in alpha oscillatory power reflect an active retinotopic mechanism for distracter suppression during sustained visuospatial attention. J. Neurophysiol. 95, 3844–3851. doi:10.1152/jn.01234.2005

Kinsbourne, M., 1977. Hemi-neglect and hemisphere rivalry. Adv Neurol 18, 41–49.

Klimesch, W., 2012. α-band oscillations, attention, and controlled access to stored information. Trends Cogn. Sci. (Regul. Ed.) 16, 606–617. doi:10.1016/j.tics.2012.10.007

Klimesch, W., 2011. Evoked alpha and early access to the knowledge system: the P1 inhibition timing hypothesis. Brain Res. 1408, 52–71. doi:10.1016/j.brainres.2011.06.003

Kok, P., Jehee, J.F.M., de Lange, F.P., 2012. Less is more: expectation sharpens representations in the primary visual cortex. Neuron 75, 265–270. doi:10.1016/j.neuron.2012.04.034

Linkenkaer-Hansen, K., Nikulin, V.V., Palva, S., Ilmoniemi, R.J., Palva, J.M., 2004. Prestimulus oscillations enhance psychophysical performance in humans. J. Neurosci. 24, 10186–10190. doi:10.1523/JNEUROSCI.2584-04.2004

Lipton, M.L., Fu, K.-M.G., Branch, C.A., Schroeder, C.E., 2006. Ipsilateral Hand Input to Area 3b Revealed by Converging Hemodynamic and Electrophysiological Analyses in Macaque Monkeys. J. Neurosci. 26, 180–185. doi:10.1523/JNEUROSCI.1073-05.2006

Lorist, M.M., Bezdan, E., ten Caat, M., Span, M.M., Roerdink, J.B.T.M., Maurits, N.M., 2009. The influence of mental fatigue and motivation on neural network dynamics; an EEG coherence study. Brain Res. 1270, 95–106. doi:10.1016/j.brainres.2009.03.015

Luck, S.J., 1995. Multiple mechanisms of visual-spatial attention: recent evidence from human electrophysiology. Behav. Brain Res. 71, 113–123.

Luck, S.J., Heinze, H.J., Mangun, G.R., Hillyard, S.A., 1990. Visual event-related potentials index focused attention within bilateral stimulus arrays. II. Functional dissociation of P1 and N1 components. Electroencephalogr Clin Neurophysiol 75, 528–542.

Luck, S.J., Hillyard, S.A., Mouloua, M., Woldorff, M.G., Clark, V.P., Hawkins, H.L., 1994. Effects of spatial cuing on luminance detectability: psychophysical and electrophysiological evidence for early selection. J Exp Psychol Hum Percept Perform 20, 887–904.

MacLean, K.A., Aichele, S.R., Bridwell, D.A., Mangun, G.R., Wojciulik, E., Saron, C.D., 2009. Interactions between endogenous and exogenous attention during vigilance. Atten Percept Psychophys 71, 1042–1058. doi:10.3758/APP.71.5.1042

Mangun, G.R., Hillyard, S.A., 1991. Modulations of sensory-evoked brain potentials indicate changes in perceptual processing during visual-spatial priming. J Exp Psychol Hum Percept Perform 17, 1057–1074.

Mangun, G.R., Hopfinger, J.B., Kussmaul, C.L., Fletcher, E.M., Heinze, H.J., 1997. Covariations in ERP and PET measures of spatial selective attention in human extrastriate visual cortex. Hum Brain Mapp 5, 273–279. doi:10.1002/(SICI)1097-0193(1997)5:4<273::AID-HBM12>3.0.CO;2-F

Mumford, D., 1992. On the computational architecture of the neocortex. Biol. Cybern. 66, 241–251. doi:10.1007/BF00198477

Newman, D.P., O'Connell, R.G., Bellgrove, M.A., 2013. Linking time-on-task, spatial bias and hemispheric activation asymmetry: a neural correlate of rightward attention drift. Neuropsychologia 51, 1215–1223. doi:10.1016/j.neuropsychologia.2013.03.027

Noesselt, T., Hillyard, S.A., Woldorff, M.G., Schoenfeld, A., Hagner, T., Jäncke, L., Tempelmann, C., Hinrichs, H., Heinze, H.-J., 2002. Delayed striate cortical activation during spatial attention. Neuron 35, 575–587.

Rajagovindan, R., Ding, M., 2011. From prestimulus alpha oscillation to visual-evoked response: an inverted-U function and its attentional modulation. J Cogn Neurosci 23, 1379–1394. doi:10.1162/jocn.2010.21478

Rauss, K., Schwartz, S., Pourtois, G., 2011. Top-down effects on early visual processing in humans: A predictive coding framework. Neuroscience & Biobehavioral Reviews 35, 1237–1253. doi:10.1016/j.neubiorev.2010.12.011

Rihs, T.A., Michel, C.M., Thut, G., 2007. Mechanisms of selective inhibition in visual spatial attention are indexed by alpha-band EEG synchronization. Eur. J. Neurosci. 25, 603–610. doi:10.1111/j.1460-9568.2007.05278.x

Ritter, W., Simson, R., Vaughan, H.G., Macht, M., 1982. Manipulation of Event-Related Potential Manifestations of information Processing Stages. Science, New Series 218, 909–911.

Rouder, J.N., Speckman, P.L., Sun, D., Morey, R.D., Iverson, G., 2009. Bayesian t tests for accepting and rejecting the null hypothesis. Psychon Bull Rev 16, 225–237. doi:10.3758/PBR.16.2.225

Sauseng, P., Klimesch, W., Stadler, W., Schabus, M., Doppelmayr, M., Hanslmayr, S., Gruber, W.R., Birbaumer, N., 2005. A shift of visual spatial attention is selectively associated with human EEG alpha activity. Eur. J. Neurosci. 22, 2917–2926. doi:10.1111/j.1460-9568.2005.04482.x

Schroeder, C.E., Mehta, A.D., Givre, S.J., 1998. A spatiotemporal profile of visual system activation revealed by current source density analysis in the awake macaque. Cereb. Cortex 8, 575–592.

Slagter, H.A., Kok, A., Mol, N., Talsma, D., Kenemans, J.L., 2005. Generating spatial and nonspatial attentional control: An ERP study. Psychophysiology 42, 428–439. doi:10.1111/j.1469-8986.2005.00304.x

Slagter, H.A., Weissman, D.H., Giesbrecht, B., Kenemans, J.L., Mangun, G.R., Kok, A., Woldorff, M.G., 2006. Brain regions activated by endogenous preparatory set shifting as revealed by fMRI. Cogn Affect Behav Neurosci 6, 175–189.

Summerfield, C., Egner, T., 2009. Expectation (and attention) in visual cognition. Trends Cogn. Sci. (Regul. Ed.) 13, 403–409. doi:10.1016/j.tics.2009.06.003

Talsma, D., Mulckhuyse, M., Slagter, H.A., Theeuwes, J., 2007. Faster, more intense! The relation between electrophysiological reflections of attentional orienting, sensory gain control, and speed of responding. Brain Res. 1178, 92–105. doi:10.1016/j.brainres.2007.07.099

Talsma, D., Slagter, H.A., Nieuwenhuis, S., Hage, J., Kok, A., 2005. The orienting of visuospatial attention: an event-related brain potential study. Brain Res Cogn Brain Res 25, 117–129. doi:10.1016/j.cogbrainres.2005.04.013

Taylor, M.M., Creelman, C.D., 1967. PEST: Efficient Estimates on Probability Functions. The Journal of the Acoustical Society of America 41, 782–787. doi:10.1121/1.1910407

Thut, G., Nietzel, A., Brandt, S.A., Pascual-Leone, A., 2006. α-Band Electroencephalographic Activity over Occipital Cortex Indexes Visuospatial Attention Bias and Predicts Visual Target Detection. J. Neurosci. 26, 9494–9502. doi:10.1523/JNEUROSCI.0875-06.2006

Van Dijk, H., Schoffelen, J.-M., Oostenveld, R., Jensen, O., 2008. Prestimulus oscillatory activity in the alpha band predicts visual discrimination ability. J. Neurosci. 28, 1816–1823. doi:10.1523/JNEUROSCI.1853-07.2008

Vogel, E.K., Luck, S.J., 2000. The visual N1 component as an index of a discrimination process. Psychophysiology 37, 190–203.

Vossel, S., Thiel, C.M., Fink, G.R., 2006. Cue validity modulates the neural correlates of covert endogenous orienting of attention in parietal and frontal cortex. NeuroImage 32, 1257–1264. doi:10.1016/j.neuroimage.2006.05.019

Wieneke, G.H., Deinema, C.H.A., Spoelstra, P., Van Leeuwen, W.S., Versteeg, H., 1980. Normative spectral data on alpha rhythm in male adults. Electroencephalography and Clinical Neurophysiology 49, 636–645. doi:10.1016/0013-4694(80)90404-6

Wijers, A.A., Lange, J.J., Mulder, G., Mulder, L.J.M., 1997. An ERP study of visual spatial attention and letter target detection for isoluminant and nonisoluminant stimuli. Psychophysiology 34, 553–565. doi:10.1111/j.1469-8986.1997.tb01742.x

Woldorff, M.G., Fox, P.T., Matzke, M., Lancaster, J.L., Veeraswamy, S., Zamarripa, F., Seabolt, M., Glass, T., Gao, J.H., Martin, C.C., Jerabek, P., 1997. Retinotopic organization of early visual spatial attention effects as revealed by PET and ERPs. Hum Brain Mapp 5, 280–286. doi:10.1002/(SICI)1097-0193(1997)5:4<280::AID-HBM13>3.0.CO;2-I

Worden, M.S., Foxe, J.J., Wang, N., Simpson, G.V., 2000. Anticipatory biasing of visuospatial attention indexed by retinotopically specific alpha-band electroencephalography increases over occipital cortex. J. Neurosci. 20, RC63.

Zhang, Y., Ding, M., 2010. Detection of a weak somatosensory stimulus: role of the prestimulus mu rhythm and its top-down modulation. J Cogn Neurosci 22, 307–322. doi:10.1162/jocn.2009.21247

Figure and legends

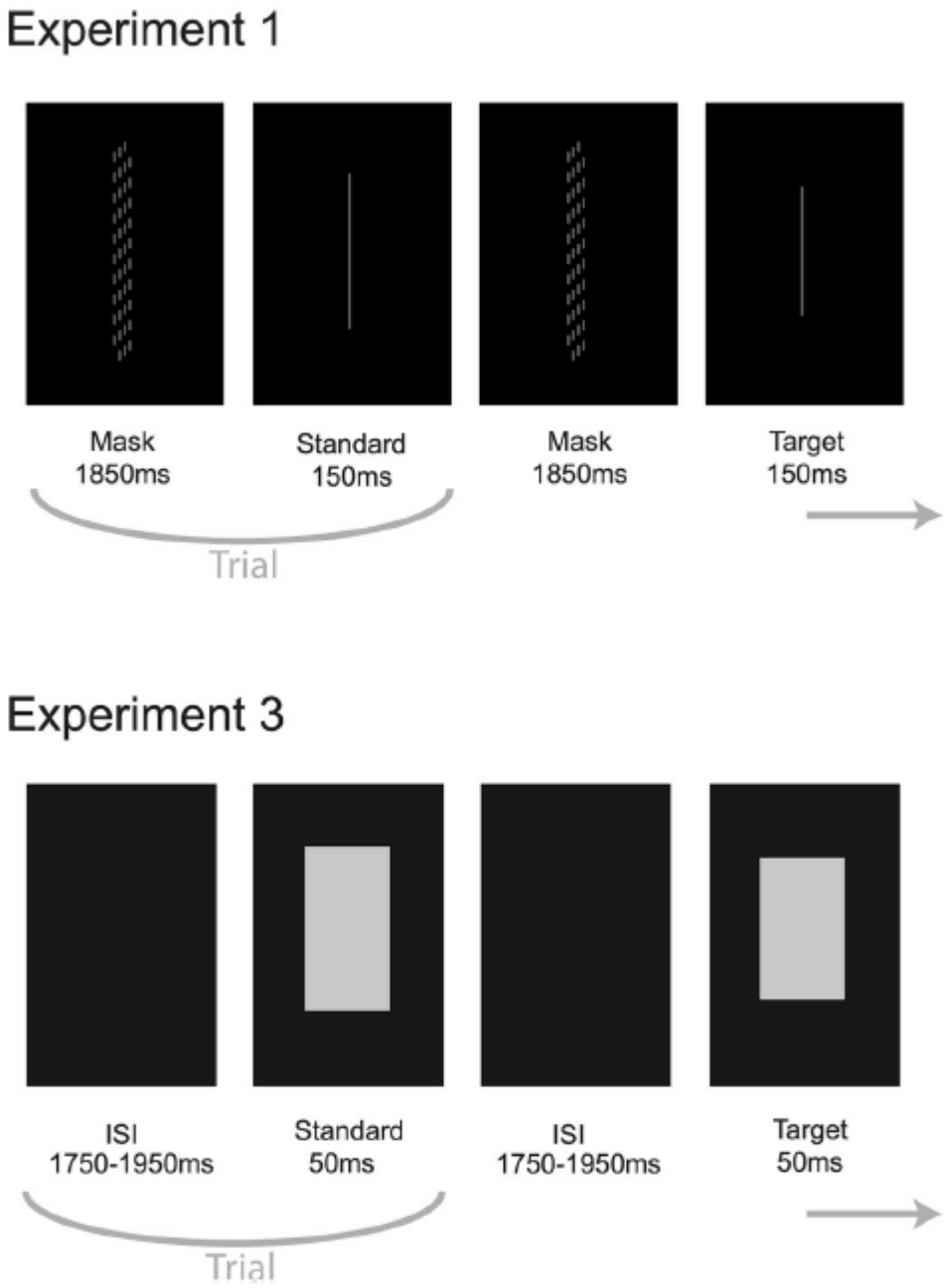

Fig. 1. Stimuli used in the continuous attention tasks in Experiment 1 (top) and Experiment 3 (bottom). Participants were asked to covertly direct their attention to one location in space either to the bottom left or bottom right of fixation where stimuli were briefly presented (about) every 2 s. Participants had to press a button whenever a rare target (shorter line/rectangle) was presented. Thus, attention was continuously directed to one hemifield. Stimuli were only presented at the attended location. In Experiment 1, during the inter-stimulus-interval (ISI) a mask pattern served as a placeholder for attention. An example of two successive stimulus trials is shown.

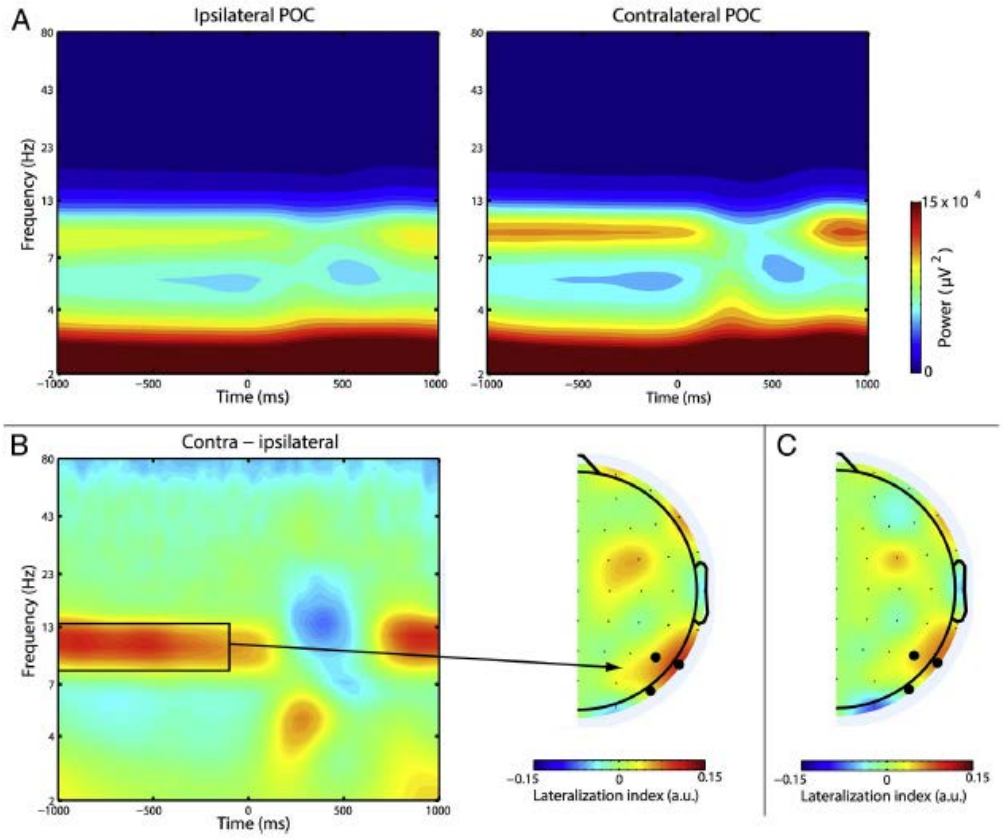

Fig. 2. Experiment 1: pre-stimulus alpha activity. A. Raw power at ipsilateral and contralateral posterior occipital cortex (POC) is shown for Correct Rejection trials as a function of time ar frequency. As can be seen, pre-stimulus alpha power was more pronounced over contralateral (relevant) vs. ipsilateral (irrelevant) posterior regions. B. This panel displays the difference power between contralateral (right) and ipsilateral (left) POC over time as a function of frequency, as well as the topography of the whole-head alpha lateralization index in Correct R jection trials, in which alpha power values at every ipsilateral electrode were subtracted from its contralateral hemisphere equivalent (e.g. PO8–PO7, C4–C3), and normalized by total alp power at both hemispheres. As can be seen, continuous attention to one hemifield was associated with relative greater alpha power over contralateral (right) vs. ipsilateral (left) POC sp cifically. This flip in alpha lateralization was already present during the first 5 min of the task (C).

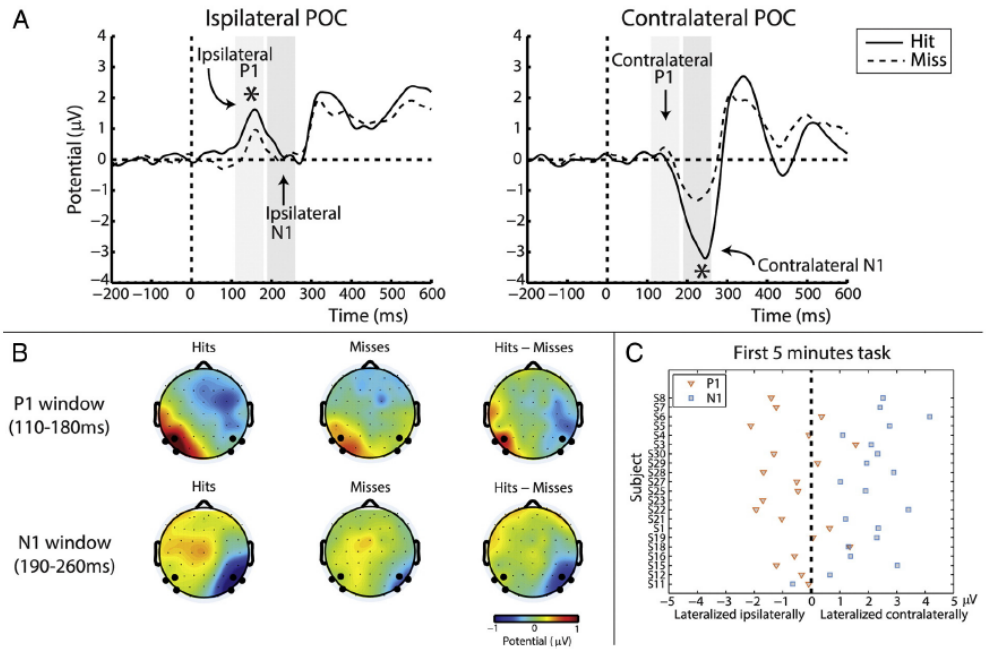

Fig. 3. Experiment 1: effects of continuous attention to one hemifield on early stimulus processing, as indexed by the P1 and N1. A. ERPs elicited by detected (hit) and undetected (miss) target stimuli over ipsilateral and contralateral posterior occipital cortex (POC). Note that the P1 and N1, as well as their attentional modulations, were perfectly lateralized to, respectively, ipsilateral and contralateral POC. B. Scalp distributions of the P1 and N1 in Hit and Miss trials, and the difference in P1 and N1 amplitude between detected and undetected left targets. This panel shows that the P1 attention effect lateralized to ipsilateral scalp regions, and the N1 attention effect to contralateral scalp regions. C. The lateralization of the P1 and N1 components was visible for most subjects already within the first 5 min of the task. Here, P1 and N1 amplitudes were based on correct rejection trials, as the number of Hit and Miss trials during the first 5 min of the task were too low to obtain reliable ERPs.

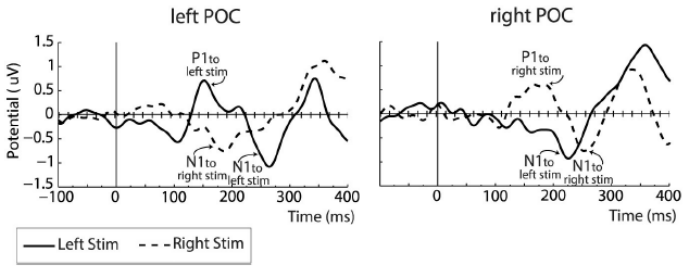

Fig. 4. Experiment 2. Under passive viewing conditions, unilateral stimuli were associated with a bilateral N1, as expected, but the P1 remained lateralized to ipsilateral scalp regions (that is, for left stimuli a P1 is only observed over left POC, and for right stimuli a P1 is only observed over right POC).

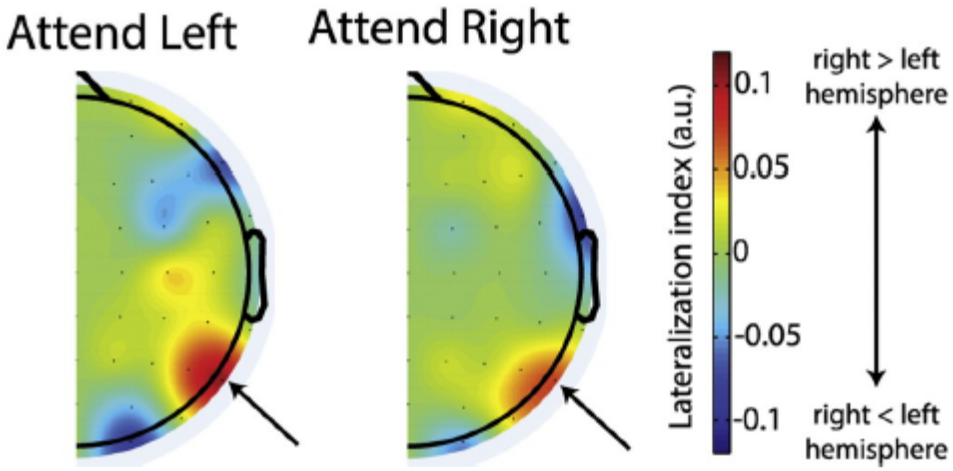

Fig. 5. Experiment 3: pre-stimulus alpha activity. Pre-stimulus alpha power was more pronounced over right vs. left posterior regions both when attention was continuously directed to the left (left panel) and when it was continuously directed to the right (right panel). Shown are the topographies of the whole-head alpha lateralization index, in which alpha power values at every left electrode were subtracted from its right hemisphere equivalent (e.g. PO8–PO7, C4–C3), and normalized by total alpha power at both electrodes (hemispheres). This was done for correct rejection trials and separately for the two attention conditions.

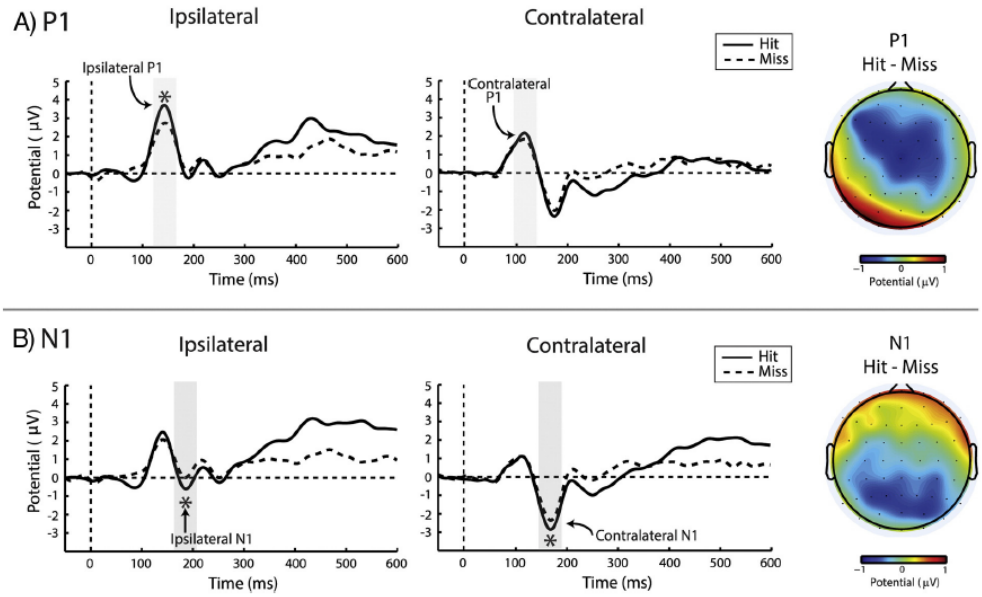

Fig. 6. Effects of continuous attention to one hemifield on early stimulus processing in Experiment 3. A: Effects on the P1 (electrodes PO7/8, P7/8, P5/6). Using different stimuli, in Experiment 3, the P1 attention effect was again lateralized to ipsilateral POC The scalp topography displays the difference in activity between Hit and Miss trials in the P1 window. B: Effects on the N1 (electrodes PO3/4, P3/4, P5/6). In contrast to the P1, the N1 was modulated by attention over both contralateral and ipsilateral scalp regions. The scalp topography displays the difference in activity between Hit and Miss trials in the N1 window.