Alpha Oscillations Correlate with the Successful Inhibition of Unattended Stimuli

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Abstract

■ Because the human visual system is continually being bombarded with inputs, it is necessary to have effective mechanisms for filtering out irrelevant information. This is partly achieved by the allocation of attention, allowing the visual system to process relevant input while blocking out irrelevant input. What is the physiological substrate of attentional allocation? It has been proposed that alpha activity reflects functional inhibition. Here we asked if inhibition by alpha oscillations has behavioral consequences for suppressing the perception of unattended input. To this end, we investigated the influence of alpha activity on motion processing in two attentional conditions using magnetoencephalography. The visual stimuli used consisted of two random-dot kinematograms presented simultaneously to the left and right visual hemifields. Subjects were cued to covertly attend the left or right kinematogram. After 1.5 sec, a second cue tested whether subjects could report the direction of coherent motion in the attended (80%) or unattended hemifield (20%). Occipital alpha power was higher contralateral to the unattended side than to the attended side, thus suggesting inhibition of the unattended hemifield. Our key finding is that this alpha lateralization in the 20% invalidly cued trials did correlate with the perception of motion direction: Subjects with pronounced alpha lateralization were worse at detecting motion direction in the unattended hemifield. In contrast, lateralization did not correlate with visual discrimination in the attended visual hemifield. Our findings emphasize the suppressive nature of alpha oscillations and suggest that processing of inputs outside the field of attention is weakened by means of increased alpha activity. ■

INTRODUCTION

The functional role of alpha oscillations has been under investigation since the discovery of EEG by Hans Berger in the late 1920s (Berger, 1929), and the properties of alpha oscillations have been described in numerous EEG and magnetoencephalography (MEG) studies (for a review, see e.g., Klimesch, 1999; Pfurtscheller & da Silva, 1999; Pfurtscheller, Stancak, & Neuper, 1996). Although it has been hypothesized that alpha activity merely reflects cortical idling, more recent work suggests that, first, alpha activity can be actively modulated, for example, by the focus of attention (see e.g., Kelly, Lalor, Reilly, & Foxe, 2006; Thut, Nietzel, Brandt, & Pascual-Leone, 2006; Yamagishi et al., 2003; Fu et al., 2001; Worden, Foxe, Wang, & Simpson, 2000), by task difficulty (Händel, Lutzenberger, Thier, & Haarmeier, 2007; Jensen, Gelfand, Kounios, & Lisman, 2002; Klimesch, Doppelmayr, Schwaiger, Auinger, & Winkler, 1999), and by memory load (Leiberg, Lutzenberger, & Kaiser, 2006; Jensen et al., 2002; Klimesch et al., 1999), and second, it has been proposed that alpha activity serves to suppress the processing of sensory information. This notion has been developed into the alpha-inhibition hypothesis, proposing that low alpha activity is a signature of regions engaged in active neuronal processing, whereas strong alpha oscillations reflect the inhibition and disengagement of task-irrelevant cortical areas (for a review, see Klimesch, Sauseng, & Hanslmayr, 2007). Such inhibition could be controlled by a top–down drive from the intraparietal sulcus or the frontal-eye field (Capotosto, Babiloni, Romani, & Corbetta, 2009). Unfortunately, there is currently no clear understanding of the physiological mechanism underlying alpha oscillations and its possible inhibitory function. However, a recent study by Lörincz, Kekesi, Juhasz, Crunelli, and Hughes (2009) proposed that the alpha rhythm can regulate processing by means of a neuronal mechanism, phasically modulating the visual input. They identified high-threshold bursting thalamocortical cells in the LGN that fired rhythmically at 10 Hz. This rhythmic firing paced inhibitory cells, which then phasically modulated thalamocortical cells exhibiting relay mode firing. As a consequence, the transmission of visual input to the neocortex was inhibited at some phases while being facilitated at others. The interpretation of alpha as an inhibitory activity is dependent on the spatial specificity of alpha because functional inhibition will only be beneficial if it is produced in task-irrelevant regions and reduced in task-relevant regions. That alpha power can decrease specifically over task-relevant areas has been reported for several modalities. The occipital alpha rhythm has been shown to decrease if visual input is presented (Aranibar & Pfurtscheller, 1978) and the so-called "mu rhythm," a 10-Hz oscillation over the sensorimotor cortical area, is reduced before and during movement execution (Pfurtscheller, Neuper, & Krausz,

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2000; Toro et al., 1994). Comparably, the tau rhythm, a 10-Hz oscillation over the auditory (midtemporal) cortical area, decreases modality-specifically, that is, only when auditory stimuli are presented (Lehtelä, Salmelin, & Hari, 1997). More recent studies have shown that the alpha power increase is also a local phenomenon that occurs specifically over task-irrelevant cortical areas. For instance, Fu et al. (2001) and Foxe, Simpson, and Ahlfors (1998) used an intermodal selective attention paradigm to demonstrate that a cue, indicating an upcoming auditory stimulus, increased alpha activity over the parieto-occipital cortex compared with a cue indicating a visual target. Furthermore, it has been shown that spatial shifts of covert visual attention were paralleled by sustained focal increases of alpha activity in a retinotopically specific manner: Increases in alpha power were observed ipsilateral to the attended hemifield (Rihs, Michel, & Thut, 2007; Kelly et al., 2006; Yamagishi et al., 2003; Worden et al., 2000). Local specificity was also shown in a recent study revealing parieto-occipital alpha power during retention of face identities, engaging the ventral stream. Conversely, parieto-occipital alpha power was reduced during the retention of face orientations, engaging the dorsal stream (Jokisch & Jensen, 2007). In the somatosensory domain, Haegens, Osipova, Oostenveld, and Jensen (2010) showed an increase over somatosensory areas ipsilateral to the hand to which the task-specific somatosensory stimulation was applied. Taken together, these experiments suggest that alpha power decreases and increases over task-relevant and task-irrelevant areas, respectively, depend on the task at hand. The question remains whether alpha activity primarily acts by decreasing in task-relevant regions, thus enhancing processing, or by increasing in task-irrelevant regions, thus inhibiting processing.

That alpha activity plays a strong role in sensory processing is clear from several reports showing that the level of posterior alpha activity before stimulus onset predicts perceptual performance. Specifically, it was shown that high prestimulus alpha power was predictive of reduced visual detection performance (van Dijk, Schoffelen, Oostenveld, & Jensen, 2008; Hanslmayr et al., 2007; Babiloni, Bultrini, Luca Romani, & Rossini, 2006; Ergenoglu et al., 2004); however, for reverse results, see Babiloni et al., 2006). It is interesting to note that in both the attentional and the perceptual paradigms mentioned above, alpha was quantified during a period in which visual input was absent, except for a fixation cross. This situation is fundamentally different from real-life situations where confrontation with strong and ever-changing sensory input is the norm. Alpha power, however, consistently decreases as a consequence of visual stimulation (Aranibar & Pfurtscheller, 1978). To investigate if alpha plays a general role in allocating resources, it is important to ascertain whether alpha power still has consequences for subsequent perception, despite strong visual input.

The aims of the current study were to further explore the functional role of alpha activity. Our first aim was to investigate if alpha activity produced in the hemisphere contralateral to the attended hemifield would lead to a decrease in performance when detection was probed in the unattended hemifield. A positive outcome would considerably strengthen the hypothesis that alpha activity serves to actively protect relevant processes by inhibiting less relevant input. The second aim was to investigate if the modulations of posterior alpha activity by attention would persist during strong visual input. If so, it would give further support to the hypothesis that alpha activity plays an important modulatory role in visual processing in real-life situations.

An account of this data has been previously given (Händel, Lutzenberger, Thier, & Haarmeier, 2008), focusing on the modulation of neuromagnetic brain responses by motion strength, that is, the coherence level of visually presented moving random dots and the influence of attention on this response modulation during the presentation of motion. It was reported that attention directed to a given hemifield increased and decreased the coherence modulation of the amplitude of an ongoing delta oscillation (3 ± 2 Hz) over the contralateral and the ipsilateral visual cortex, respectively, suggesting changes in the signal-to-noise ratio at the neural population level because of attention.
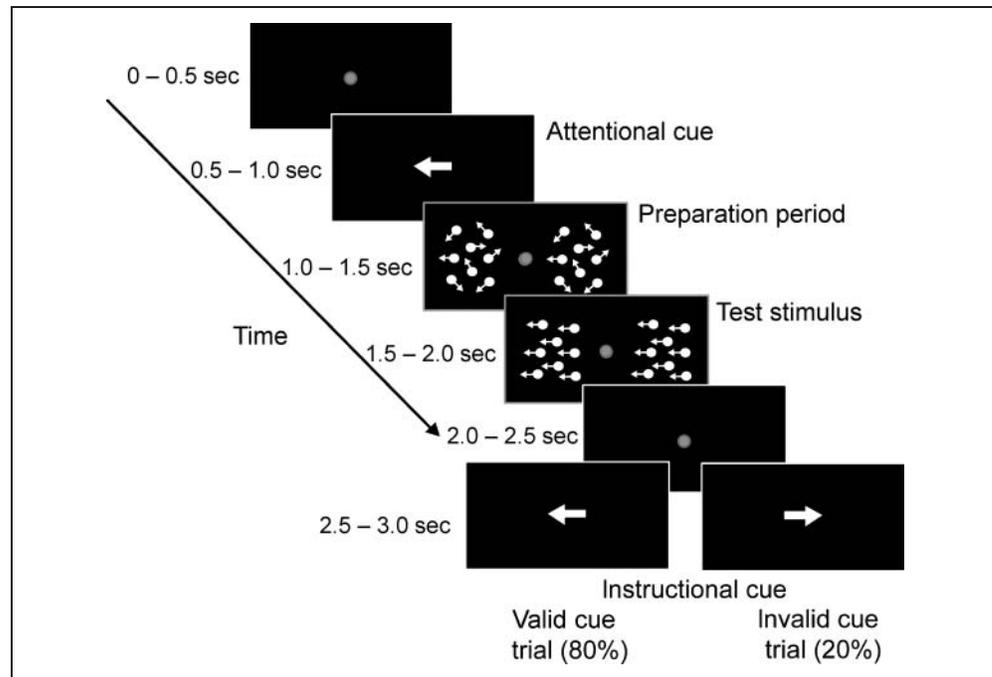
METHODS

Nine healthy subjects (eight women), with a mean age of 23 ± 3 years, participated in the study. All subjects had normal or corrected-to-normal vision. Informed consent was obtained from all subjects according to the Declaration of Helsinki and the guidelines of the Ethics Committee of the Faculty of Medicine of the University of Tübingen, which approved the study and where the experiments were conducted.

Psychophysical Task and Eye-movement Control

Subjects were seated upright in a magnetically shielded room (Vakuum-Schmelze, Hanau, Germany) and were instructed to sit as motionless as possible during the MEG recording. Stable posture was supported by a chin rest attached to the MEG chair. The computer-generated visual stimuli were rear projected onto a large translucent screen (DLP projector, frame rate 60 Hz, 800 × 600 pixels) positioned at a viewing distance of 92 cm in the magnetically shielded room. Viewing was binocular.

The trials were composed of six periods, each lasting 0.5 sec (see Figure 1). After a baseline fixation period (central fixation dot, diameter 10 arcmin), an arrow ("attentional cue") instructed subjects to covertly direct attention either to the left or to the right hemifield. The attentional cue was followed by two random-dot kinematograms (RDKs), each covering a 16×16 deg^2 centered 15° right and left of the fixation point, respectively. The RDKs consisted of 1500 white squares (side length = 8 arcmin,

Figure 1. Experimental paradigm. The stimulus consisted of six periods each lasting 0.5 sec. After a fixation period, an arrow (attentional cue) instructed subjects to shift their attention to the left or right hemifield. The stimuli during the preparation period comprised two RDKs of incoherent motion. In the following test stimulus, dot motion was coherent as defined by the percentage of dots moving in the same direction (5%, 20%, 50%, or 100%). Global motion direction was either to the left or to the right and could be different for the two RDKs; motion coherence was identical for both sides. After a subsequent second fixation period, a second arrow (instructional cue) indicated for which of the two RDKs subjects had to indicate the direction of coherent motion (two-alternative forced choice). Valid cueing was applied in 80% of trials. Trials with predefined motion coherence (120 presentations each) served as the collection of neuromagnetic responses and were presented randomly interleaved with trials whose motion coherence was varied according to an adaptive staircase procedure to determine the psychophysical thresholds.

lifetime = 1 sec, dot density = ~6 dots/deg^2, luminance = 47 cd/m^2), all moving incoherently, that is, in all possible directions with a resolution of 1°, at a common speed of 6 deg/sec. After the presentation of this first pair of RDKs (the "preparation period"), a second pair of RDKs, the "test stimulus," started. The properties of the test stimulus were identical to those described for the preparation period, except that a certain percentage of the dot elements moved coherently in the same direction (either to the left or to the right). Specifically, the percentage of coherently moving dots was either 5%, 20%, 50%, or 100% of all dots in an individual trial. Although the amount of motion coherence was always identical for the two RDKs in a given trial, global motion direction could be the same or different as randomly chosen by the computer. After a subsequent second fixation period, a second arrow (the "instructional cue") indicated for which of the two RDKs subjects had to indicate the direction of coherent motion (two-alternative forced choice). Valid cueing, as defined by congruent orientation of the attentional and the instructional cue, was applied in 80% of the trials. Trials with a valid cue could show either predefined motion coherence (four levels, 120 presentations each) or motion coherence that varied according to an adaptive staircase procedure. Invalidly cued trials showed only adaptive coherence levels. Neuromagnetic signals were only collected for the validly cued trials with predefined motion coherence. These trials were randomly interleaved with trials where the motion coherence was varied according to an adaptive staircase procedure to determine two psychophysical thresholds: one for the condi-

tion of valid instructional cueing and the other for the invalid instructional cueing. To assess the ability to discriminate the motion direction embedded in noise, we plotted the percentage of correct responses as a function of motion coherence and fitted the data using a probit function (McKee, Klein, & Teller, 1985). The perceptual threshold was defined by the coherence level for which the probit function predicted 75% correct responses.

During all experiments, eye movements were monitored using a custom-built video system tracking the center of the pupil as a measure of eye position. Recordings were stored at a sampling rate of 50 Hz and analyzed off-line to assess the quality of fixation. In particular, the influence of spatial orienting on the following oculomotor parameters was tested for the prestimulus period: the deviations from the fixation point (eye position in the x and y direction), the number and amplitude of saccades, and the number of eye-tracker artifacts due to failures in pupil detection (as a measure of data quality). The means of the various oculomotor measures were calculated for each subject for the preparation period and were compared between the two possible directions of the attentional cue by means of a paired t test as well as being subjected to a linear regression analysis with the perceptual thresholds.

MEG Acquisition

Neuromagnetic activity was recorded using a whole-head MEG system (CTF, Inc., Vancouver, Canada) containing

151 first-order axial magnetic gradiometers. The signals were low-pass filtered at approximately 150 Hz and sampled at a rate of 625 Hz. Recording epochs lasted from stimulus onset to arrow offset plus 0.2 sec, leaving 3.2 sec of recording time for each trial.

Two sensors (MRP31 and MRF32) were excluded from the analysis because of malfunction. Only those trials were included in the further analysis, which showed a variance (calculated over whole trial) below 2.5 times the mean variance. Data were further detrended on the basis of the whole trial, and line noise was attenuated using a 50-Hz notch filter. All analyses were done using MATLAB 7.5.0 (The MathWorks, Inc., Natick, MA) and the Fieldtrip software package (http://www.ru.nl/fcdonders/fieldtrip/, a Matlab-based toolbox for the analysis of electrophysiological data). Furthermore, each trial was normalized by dividing every single sensor with the mean over all the sensors for each frequency band and sample (except when described as raw power).

To optimize analysis over subjects on the sensor level, we converted axial gradiometer information into planar gradients (van Dijk et al., 2008; Bastiaansen & Knosche, 2000). The horizontal and vertical components of the planar gradients were estimated at each sensor location using the fields from the specific sensor and its neighboring sensors. Importantly, the power values for the horizontal and vertical components were summed for each sensor location after the spectral analysis. Planar gradiometers mostly display activity from sources that lie beneath the peak of the activation, whereas for the axial sensors, a single source would be displayed as a bipolar pattern. In that case, the sensors showing peak activation might lie far away from the actual source, dependent on how deep in the brain it is localized (Hämäläinen, Hari, Ilmoniemi, Knuutila, & Lounasmaa, 1993). The shape and the characteristic of this pattern are greatly dependent on the orientation of the source. As a consequence, activation at identical sites, but with different orientations, might give rise to a quite different spatial distribution of activity. Changing the signal to a planar representation can therefore be very beneficial for comparing activity between subjects on a sensor level.

Time-frequency representations of power (1–30 Hz, 0–3 sec) were calculated using a Hanning window and fast Fourier transforms. The analysis window had a length of 0.5 sec and was shifted in steps of 0.1 sec, with a first center point at 0.25 sec and the last at 2.45 sec covering the prestimulus interval. Alpha activity between 9 and 13 Hz was used for further analysis. First, the mean was calculated for the time points averaged over the cue period, the prestimulus period, and the test stimulus period. We then applied t tests over the mean of all the sensors contralateral to the attended side minus all the sensors ipsilateral to the attended side. Second, for each hemisphere, the four neighboring sensors that displayed the highest difference in the positive or negative power values in the group data between the two conditions (attention left vs. right) were

selected. For these two sensor groups, a lateralization index was calculated for each subject as

$$k_{\text{lateralization}} = \frac{\text{power}(f)_{\text{ipsilateral}} - \text{power}(f)_{\text{contralateral}}}{\text{power}(f)_{\text{ipsilateral}} + \text{power}(f)_{\text{contralateral}}}$$

(alpha power ipsilateral means power values collected in the sensors ipsilateral to the attended hemifield). The lateralization index was then averaged over the two conditions (i.e., attention left and right). Furthermore, a linear regression over subjects was calculated over the lateralization index and the perceptual threshold of the cued and the uncued side, respectively. This regression was additionally calculated for the right and the left sensors, separately. In that case, the lateralization index was also calculated separately for the left and the right sensors; for example, power in the left sensors during attention directed to the left side minus power in the left sensors during attention directed to the right side divided by the sum.

RESULTS

Subjects correctly directed covert attention to the cued side, as indicated by the fact that valid cueing resulted in perceptual thresholds of 18% (percentage of coherently moving dots required to obtain 75% correct responses) as opposed to 44% for the invalidly cued trials (paired t test, $p < .01$). Eye-tracker recordings showed that subjects' fixation during the preparation interval was on average less than half a degree shifted to the right for both cue directions, with a bias toward the right cue (left, 0.1°; right, 0.5°; paired t test, p corrected for multiple comparison $p < .02$). No other oculomotor parameter (deviation from the fixation point in the horizontal direction, number and amplitude of saccades, and number of eye-tracker artifacts) showed a significant difference with respect to the direction of the attentional cue. Importantly, there was no linear relationship with the perceptual threshold obtained for the cued or the uncued side ($p_{\text{uncorrected}} > .35$).

To characterize the change in oscillatory brain activity with respect to the attentional cue, we calculated the time-frequency representations of power. Figure 2A shows the evolution of raw power for 4–30 Hz for the sensors ipsilateral (left panel) and contralateral (right panel) to the attended side. For both the sensor groups, we observed a strong modulation in the 10-Hz alpha band, which was mainly a reduction in alpha power after the onset of the incoherent motion stimulus (the preparation interval). This behavior can be seen in detail in Figure 2B, which shows the time course specifically for the 10-Hz raw power for the ipsilateral (blue line) and the contralateral (red line) sensors. To visualize the difference in power between the ipsilateral and the contralateral sensors, we plotted the time-frequency representation of the lateralization index (see Methods section; Figure 2D). Mainly during the
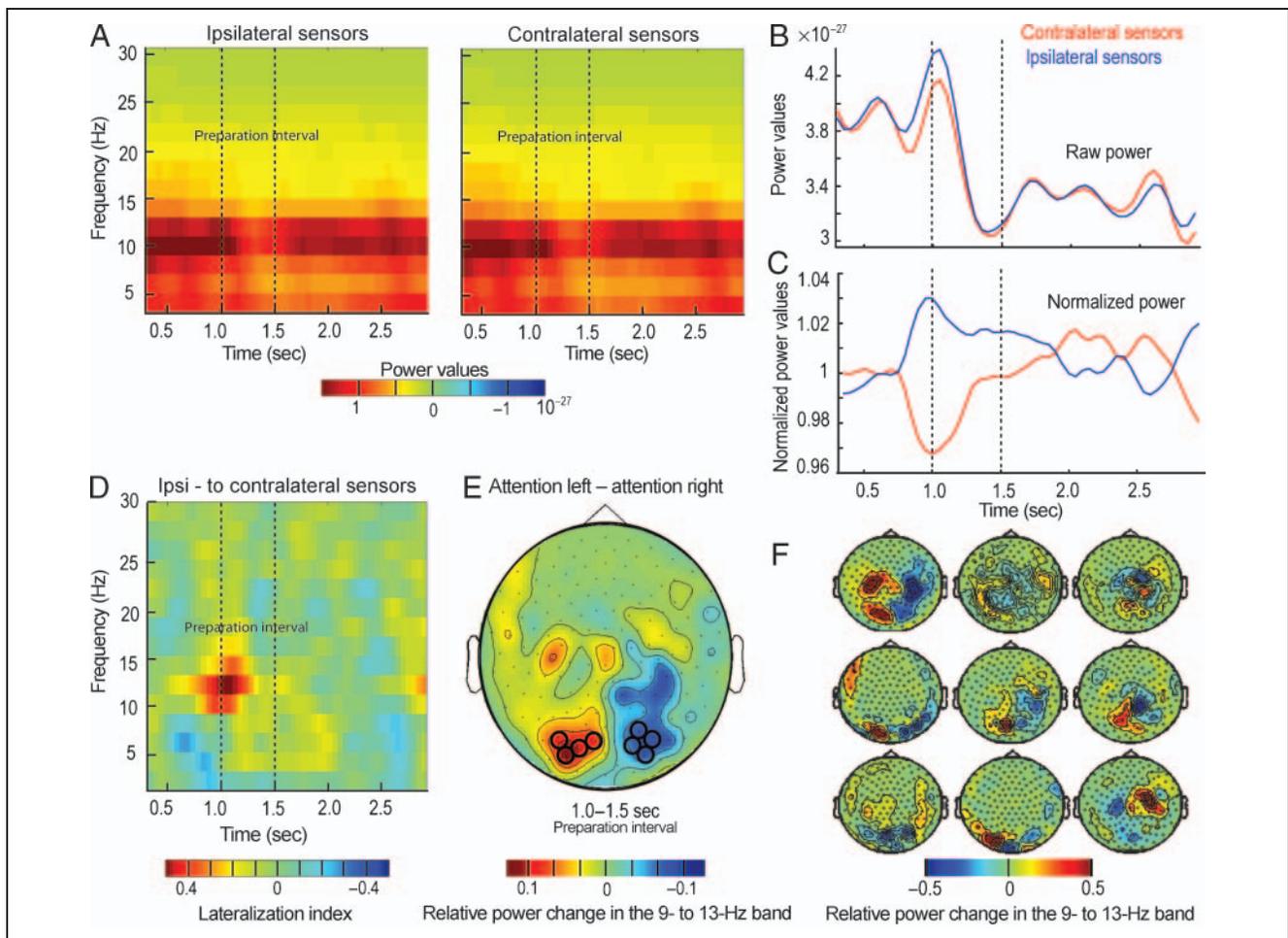
Figure 2. (A) Time-frequency plots of all sensors located ipsilateral (left figure) or contralateral (right figure) to the attended side. The red color indicates high power, and the blue color indicates low power. Raw data without baseline correction are used for plotting. The black broken lines mark the preparation period, that is, the onset of the incoherently moving random dots. (B) Time course of the 10-Hz raw power for all ipsilateral (blue line) and all contralateral (red line) sensors. (C) Time course of the normalized 10-Hz power for all ipsilateral (blue line) and contralateral (red line) sensors. To normalize power, we divided the values of each sensor by the mean power over all sensors. Contralateral and ipsilateral power show a significant difference during the preparation period (1.0–1.5 sec, $p_{corrected} = .037$) but not during cue presentation (0.5–1.0 sec, $p_{corrected} = .59$) and test-stimulus period (1.5–2.0 sec, $p_{corrected} = .18$). (D) Time-frequency plot of the lateralization index of alpha power. The red color indicates that activity contralateral to the attended side is weaker than activity ipsilateral to the attended side. The black broken lines mark the preparation period. (E) Spatial distribution of the 9- to 13-Hz alpha range during the preparation period (1–1.5 sec). The topographical distribution (mean over all subjects) of the alpha power is plotted as the difference between trials in which attention was focused on the left hemifield compared with attention focused on the right hemifield. The red color indicates a positive difference between trials, with attention focused left versus right, whereas the blue color indicates a negative difference. (F) The topographical distribution of the difference in alpha power dependent on the focus of attention plotted for the single subjects. Same conventions as in panel E.

preparation interval, a pronounced difference in the alpha band between ipsilateral and contralateral activation can be seen. The red color indicates a positive effect, meaning that alpha power contralateral to the attended side was weaker than ipsilateral activity. This difference lasted for most of the preparation period, that is, during bilateral stimulation with incoherent motion (1.0–1.5 sec after cue offset). It should be kept in mind that the presentations during the preparation intervals were identical for both hemifields. Figure 2C shows the overall change in alpha power in all the sensors after normalization, where the power in the individual sensors was divided by the mean power over all the sensors. This normalization directs the focus on the local change

in power by attenuating the effect of global changes. As can be seen, ipsilateral alpha activity (blue line) increases after cueing, whereas alpha power in the sensors contralateral to the attended side (red line) decreases. This relationship reverses shortly before the coherent motion offset. Thus, if the effect of the overall decrease in alpha power due to the onset of the incoherently moving random-dot pattern is diminished ipsilaterally compared with contralaterally, we see an increase in alpha power for the sensors ipsilateral to the attended side. By means of a t test, we then compared the mean power over the ipsilateral with the contralateral sensors during cue presentation (0.5–1.0 sec, $p_{corrected} = .59$), preparation period (1.0–1.5 sec,

$p_{corrected} = .037$), and test stimulus period (1.5–2.0 sec, $p_{corrected} = .18$). The significant difference during the preparation period demonstrates that the alpha lateralization is robust before the test period. Figure 2E shows that the focus of this significant lateralization is distributed quite symmetrically over the posterior sensors. The alpha power change was positive in the left and negative in the right posterior sensors. This pattern as well as its spatial distribution over the parieto-occipital cortex was visible in most of the single subjects, as shown in Figure 2F. In summary, Figure 2 shows that posterior alpha activity was lateralized with respect to the direction of covert attention in such a way that the sensors ipsilateral to the attended side showed increased alpha activity whereas the sensors contralateral to the attended side showed decreased alpha activity, relative to each other. This pattern is only visible if the overall strong

alpha power decrease due to the luminance change induced by the random-dot onset is disregarded.

We then tested if the strength of the lateralization effect was related to the perceptual ability of the subjects. The perceptual thresholds were estimated in a behavioral test by means of a staircase procedure for the attended and the unattended hemifields (for details, see Methods section). Figure 3 shows the individual lateralization indices plotted as a function of the individual perceptual thresholds. As can be seen in Figure 3A, there was no linear relationship between the lateralization index and the threshold for the validly cued trials ($R^2 = 0.04$, $p = .62$). On the other hand, Figure 3B reveals a strong positive linear relationship between the lateralization index and the perceptual threshold obtained from the invalidly cued trials ($R^2 = 0.76$, $p = .002$).
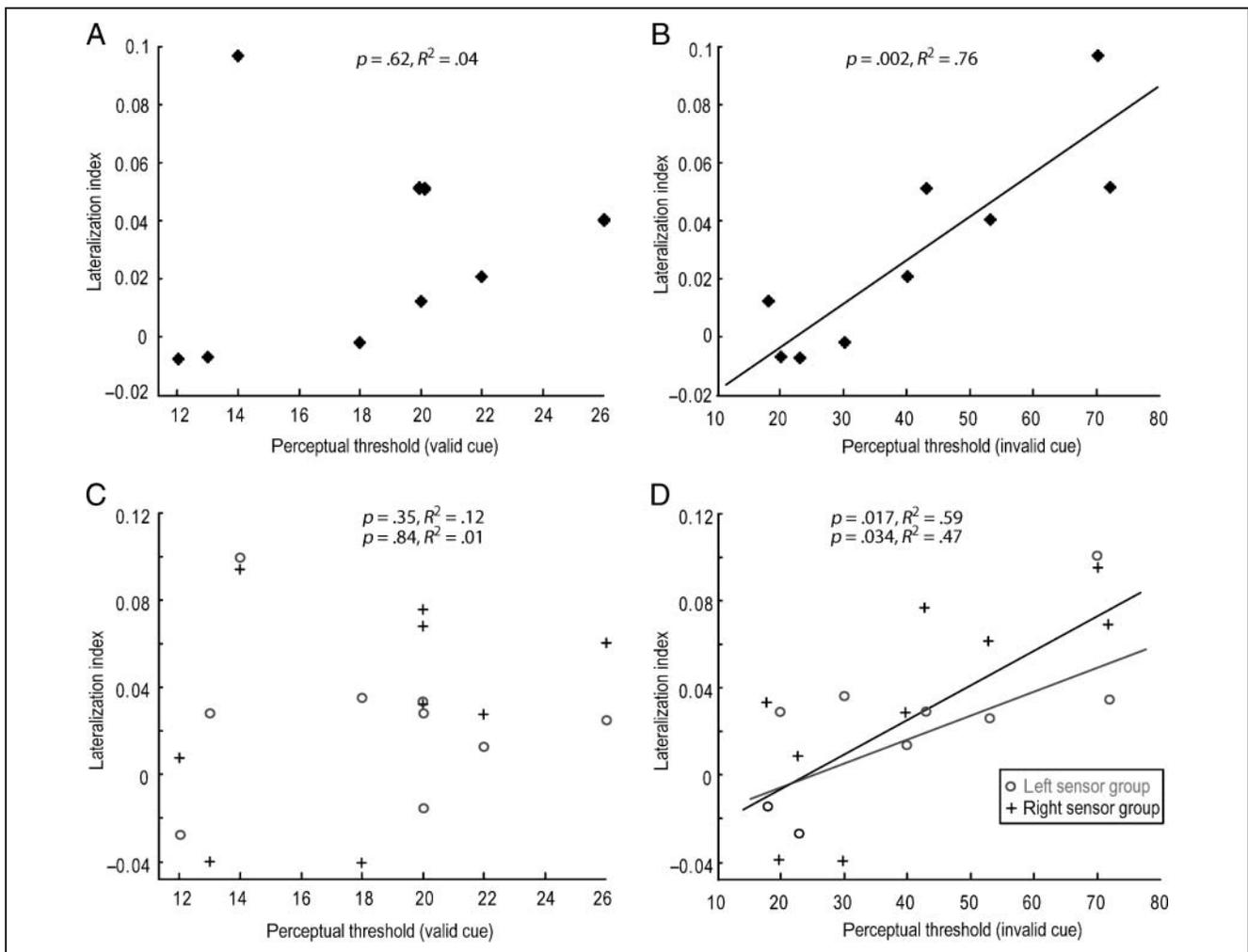
Figure 3. Individual lateralization index plotted as a function of the perceptual threshold generated by means of a staircase procedure for the validly (left panels) and the invalidly cued trials (right panels). The upper two panels show the lateralization index of the alpha power as calculated for the left and the right sensors combined. There is a strong positive linear relationship between the lateralization strength of alpha power and the perceptual threshold obtained from the invalidly cued trials (B, $R^2 = 0.76$, $p = .002$) but no relationship between lateralization and threshold for the validly cued trials (A, $R^2 = 0.04$, $p = .62$). An additional regression was calculated for right sensors (gray circles) and left sensors (black crosses) separately (see lower panels, C and D). A significant positive linear relationship was present for left (D, $R^2 = 0.59$, $p = .017$) as well as right sensors (D, $R^2 = 0.47$, $p = .034$) between the alpha lateralization and the perceptual threshold measured for the invalidly cued trials.

To investigate if this relationship was dominated by only one hemisphere, we calculated the regression for the right and the left sensors separately. To this end, we calculated the lateralization index by taking those trials with attention directed ipsilaterally to the selected sensor group and compared them with those trials directing attention contralaterally. It can be clearly seen in Figure 3D that the linear relationship was present for the left (black crosses) as well as the right (gray circles) sensors for the perceptual threshold for the invalid cues only. A significant positive linear relationship was found for the left ($R^2 = 0.59$, $p = .017$) as well as the right sensors ($R^2 = 0.47$, $p = .034$). This poorly demonstrates that subjects who detected the worst in the unattended hemifield (probably as a consequence of orienting attention according to the cue) were also the subjects with the strongest alpha power lateralization.

DISCUSSION

In the current study, subjects were instructed to attend either to the left or to the right side while random-dot fields were presented in both hemifields. The task of the subjects was to detect subtle directional changes in the movement of the dots. Analysis of brain activity recorded by MEG revealed a clearly lateralized alpha activity over the occipital cortex, with higher alpha power contralateral to the unattended side and lower alpha power contralateral to the attended side. Our key finding was that the magnitude of this lateralization predicted the performance of the subjects when they were probed to report directional changes in the unattended side.

Alpha oscillations and perceptual performance seem to be linked. Recently, it has been shown that low prestimulus alpha activity in visual areas goes hand in hand with a good performance in a visual detection task and vice versa (van Dijk et al., 2008; Hanslmayr et al., 2007; Ergenoglu et al., 2004). In addition, alpha power decreases in human and monkey visual cortex have been reported to correlate with decreasing RTs when responding to visual stimuli (Zhang, Wang, Bressler, Chen, & Ding, 2008; Thut et al., 2006). A more complex relationship was described for the somatosensory system, where medium levels of alpha-band activity preceded optimal detection (Zhang & Ding, 2010; Linkenkaer-Hansen, Nikulin, Palva, Ilmoniemi, & Palva, 2004). Another line of evidence stems from the TMS work, showing that the excitability of the cortex probed by phosphenes is dependent on alpha power (Romei, Brodbeck, et al., 2008; Romei, Rihs, Brodbeck, & Thut, 2008). These findings clearly indicate that alpha is relevant for sensory processing. However, it remains uncertain if these findings reflect an alpha increase in unengaged areas or whether they reflect a decrease in the engaged areas to enhance neuronal processing. This study provides support for the notion that alpha activity reflects an active inhibitory process: A well-known feature of the visual system is its strong hemispheric lateralization. The motion stimuli used in our study are processed in early and late motion-sensitive visual areas, which are retinotopically organized and show a lateralized response. As, for example, shown in intracranial monkey recordings from motion-sensitive area MT/V5, only the neuronal firing contralateral to the stimulated hemifield correlates with monkeys' motion perception (Newsome, Britten, & Movshon, 1989). More recent studies also show strongly lateralized responses to visual input in the human intraparietal sulcus (Gardner, Merriam, Movshon, & Heeger, 2008). Several studies have reliably localized the sources of the lateralized alpha oscillations associated with attention in various tasks to these regions (Siegel, Donner, Oostenveld, Fries, & Engel, 2008; Van Der Werf, Jensen, Fries, & Medendorp, 2008). In our study, correlation with perception in one hemifield should therefore be mainly affected by activity on the contralateral side. If only the decrease in alpha power is driving the lateralization index, no effect on the ipsilateral (in our case unattended) perception should be expected. We therefore are quite confident that an increase in alpha power contralateral to the relevant but unattended visual field exerts influence on perception. By inhibiting the processing of unattended and therefore potentially distracting sensory input at an early stage of the cortical hierarchy, alpha can act as an active filter.

An active increase of alpha ipsilateral to the attended side is in line with previous experiments showing an occipital alpha power increase compared with baseline contralateral to the ignored hemifield (Kelly et al., 2006; Yamagishi et al., 2003; Worden et al., 2000). Alpha power was also reported to be increased over parieto-occipital areas, when attention was directed to auditory input (Fu et al., 2001). Interestingly, this pronounced increase in alpha seems to be dependent on stimulus details of the task, as discussed by Thut et al. (2006). They point out that alpha power was increased over the to-be-ignored area relative to baseline in those studies in which a distractor was present in the task (Kelly et al., 2006; Yamagishi et al., 2003; Fu et al., 2001; Worden et al., 2000). If the target stimulus was presented alone, occipital alpha power was reported to decrease compared with baseline contralateral to the attended hemifield (Thut et al., 2006; Sauseng et al., 2005). In addition, occipital alpha power was described to decrease if visual input was expected (Klimesch, Russegger, Doppelmayr, & Pachinger, 1998) but not if auditory input was expected (Bastiaansen, Bocker, Brunia, de Munck, & Spekreijse, 2001). In the task at hand, two stimuli were presented, one on the cued side, that is, the target, and one on the uncued side for most of the trials a rather distracting input. Our finding of increased alpha activity contralateral to the uncued side is therefore in line with the interpretation that active suppression is realized by the brain if distracters are present.

One might ask why we did not observe an effect of alpha lateralization on performance in the attended hemifield. Or stated differently, why did efficient inhibition by alpha at the unattended site not convert into enhanced discrimination at the attended location? Arguably, the main reason

is that successful discrimination depends not only on inhibiting unattended stimuli but also on efficient processing of the attended stimuli (e.g., Golla, Ignashchenkova, Haarmeier, & Thier, 2004). In other words, we have to assume that under the experimental conditions of this study, inhibition by alpha of the unattended stimuli was not the only critical and limiting factor for discriminating stimuli at the attended location.

Another important finding of our study is that alpha lateralization was present during massive visual input. Until now, studies have almost exclusively investigated the role of alpha activity, although almost no sensory input was present. This is at odds with real-life situations where we are constantly confronted with strong and ever-changing sensory input. However, to claim that alpha oscillations play an important role in real-life situations, it is necessary to show that alpha plays a functional role in the presence of visual input. This study indicates that alpha activity is modulated by attention in the presence of strong visual input and remains a strong predictor of performance. This suggests that alpha controls resource allocation in the working brain and therefore might be important in real-life situations.

In addition, the predictive power of alpha might be used as an indicator of how well subjects can focus their attention or, to rephrase, how well they are capable of observing sensory changes despite focusing attention on something else. This might be relevant for investigating the neuronal substrate of attentional deficit disorders or for the pre-screening of subjects to be involved in jobs in which allocation of visual attentional resources is important.

In conclusion, our findings suggest that attention actively directs alpha power to impede the processing of potentially distracting input. A strong hemispheric specific alpha increase seems to result in a stronger inhibition, which worsens the perceptual performance on the unattended stimuli. Thus, alpha lateralization might be used as a measure for an individual's ability to allocate attention by suppressing distracting input.

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