Somatosensory Anticipatory Alpha Activity Increases to Suppress Distracting Input

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Abstract

■ Effective processing of sensory input in daily life requires attentional selection and amplification of relevant input and, just as importantly, attenuation of irrelevant information. It has been proposed that top–down modulation of oscillatory alpha band activity (8–14 Hz) serves to allocate resources to various regions, depending on task demands. In previous work, we showed that contralateral somatosensory alpha activity decreases to facilitate processing of an anticipated target stimulus in a tactile discrimination task. In the current study, we asked whether somatosensory alpha activity is also modulated when expecting incoming distracting stimuli on the nonattended side. We hypothesized that an ipsilateral increase of alpha to suppress distracters would be required for optimal task performance. We recorded magnetoencephalography while subjects performed a tactile stimulus discrimination task where a cue directed attention either to their left or right hand. Distracters were presented simultaneously to the unattended hand. We found that alpha power contralateral to the attended hand decreased, whereas ipsilateral alpha power increased. In addition, posterior alpha power showed a general increase. Importantly, these three alpha components all contributed to discrimination performance. This study further extends the notion that alpha band activity is involved in shaping the functional architecture of the working brain by determining the engagement and disengagement of specific regions: Contralateral alpha decreases to facilitate stimulus detection, whereas ipsilateral alpha increases when active suppression of distracters is required. Importantly, the ipsilateral alpha increase is crucial for optimal task performance. ■

INTRODUCTION

Converging evidence suggests that alpha band activity plays an important role in setting the state of sensory regions depending on task demands (Jensen & Mazaheri, 2010; Klimesch, Sauseng, & Hanslmayr, 2007; Cooper, Croft, Dominey, Burgess, & Gruzelier, 2003). In this view, alpha activity decreases to facilitate processing in task-relevant regions and increases to suppress interference from task-irrelevant regions. A substantial body of literature on visual attention has demonstrated that lateralized occipital alpha activity reflects the direction of visuospatial attention (Rihs, Michel, & Thut, 2007; Worden, Foxe, Wang, & Simpson, 2000; Foxe, Simpson, & Ahlfors, 1998) in a graded manner (Gould, Rushworth, & Nobre, 2011) and influences detection performance (Händel, Haarmeier, & Jensen, 2011; Thut, Nietzel, Brandt, & Pascual-Leone, 2006).

Recently, it was shown that anticipatory alpha activity in the somatosensory system (also referred to as "rolandic alpha" or the "mu rhythm") behaves in a similar way (Anderson & Ding, 2011; Haegens, Händel, & Jensen, 2011; Van Ede, de Lange, Jensen, & Maris, 2011; Jones et al., 2010). Somatosensory prestimulus alpha lateralization reflects allocation of attention and influences perfor-

mance: both accuracy and speed of response improve with the degree of alpha lateralization. Furthermore, by manipulating cue reliability we demonstrated that the strength of somatosensory alpha lateralization is modulated by the degree of anticipation, suggesting it is under top–down control (Haegens, Händel, et al., 2011). However, the contribution to the alpha lateralization from sensory regions contralateral and ipsilateral to the attended hand remains unclear. From the visuospatial attention literature, it seems that directing attention to the cued side mainly leads to a decrease of alpha in the contralateral hemisphere (Thut et al., 2006; Sauseng et al., 2005), whereas some studies have reported an additional ipsilateral increase reflecting the ignored location (Rihs, Michel, & Thut, 2009; Rihs et al., 2007), often in paradigms that included distracters (Kelly, Lalor, Reilly, & Foxe, 2006; Fu et al., 2001; Worden et al., 2000). The parameters and conditions determining the contralateral and ipsilateral alpha modulations are currently actively investigated.

Here, we set out to further elucidate the role of ipsilateral alpha power increase in the context of somatosensory spatial attention by manipulating distracter strength. Specifically, we asked how somatosensory alpha activity is modulated in expectation of incoming distracting stimuli on the nonattended side. We hypothesized that, in addition to a decrease of alpha activity contralateral to the attended side, an ipsilateral increase of alpha activity would

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be required for optimal task performance. Furthermore, we predicted that these alpha power modulations would increase with increasing distracter strength.

METHODS

Subjects

Twenty-four healthy, right-handed subjects (mean age = 22 years, range = 18–29 years, 18 women) participated in the experiment after giving written informed consent. The study was carried out in accordance with the guidelines of the local ethics committee and the Declaration of Helsinki. All subjects had normal or corrected-to-normal vision.

Materials

Electrical stimuli (0.2 msec) were delivered with two constant-current high-voltage stimulators (Digitimer Ltd., Hertfordshire, UK) to the left and right hand thumbs. The stimulus intensity was set to approximately 150% (mean = 3.2 mA, range = 2.0–5.5 mA) of the subject's sensory threshold level. For the condition with weak target stimuli (see below) we used 120% (mean = 2.6 mA, range = 1.5–4.7 mA) of the threshold level. These levels were established during a practice session before the recordings, for each thumb independently.

Experimental Paradigm

Subjects performed a somatosensory spatial attention task (Figure 1A), in which they were instructed to attend to their left or right hand thumb and had to discriminate the target stimulus. The task of the subject was to indicate by button press with the right index finger whether a one-pulse (lower button) or two-pulse target stimulus (upper button) was presented. Each trial consisted of a 1-sec baseline, 0.5-sec visual cue (arrow to left or right; cues were always valid), 1-sec prestimulus interval, 0.5-sec stimulus window, and, at maximum, 1.5-sec response window, followed by 0.2-sec feedback (correct response, green cross; incorrect/no response, red cross). Subjects were required to fixate at a fixation cross throughout the trial.

The experiment consisted of four conditions (block design, order counterbalanced over subjects) of 200 trials each: (1) normal target, no distracter; (2) normal target, weak distracter; (3) normal target, strong distracter; and (4) weak target, no distracter (note: the purpose of this fourth condition was to assess the effect of increased task difficulty independent of distracter presence). Throughout this article, we will refer to these conditions as "no," "weak," "strong," and "no*" distracter, respectively. The distracter consisted of a pulse train presented to the non-cued thumb. The stimulus window was of 0.5-sec length, and the target pulse(s) could be presented at 0.1 and/or 0.4 sec, whereas the distracter was presented throughout
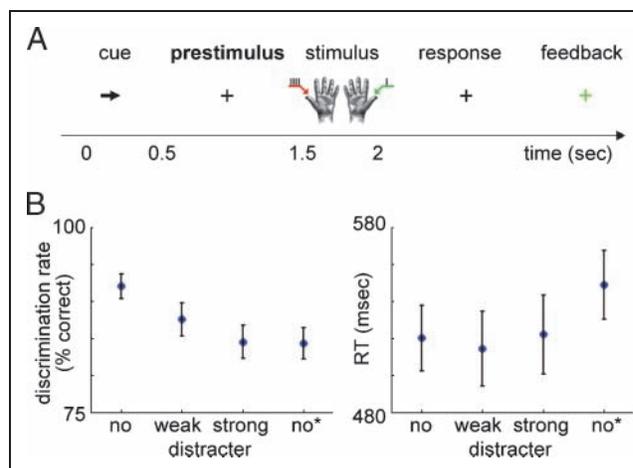

Figure 1. Experimental paradigm and behavioral results. (A) Subjects performed a tactile stimulus discrimination task where a visual cue directed attention either to their left or right hand. Subjects had to indicate whether the target stimulus consisted of one or two electrical pulses presented to the cued thumb. In the distracter conditions, a pulse train was presented to the noncued thumb (target stimulus depicted in green, distracter in red). (B) Discrimination rate (left) and RT (right) for each of the experimental conditions: no, weak, strong, or no* distracter (where "no*" refers to the condition with no distracter and weak target stimulus). There was a significant decrease of discrimination rate over conditions, although RTs did not differ significantly, except for the no* condition (see Results). Error bars indicate *SEM*.

the 0.5-sec stimulus window (strong distracter: 11 pulses at 20 Hz) or for the first 60 msec (weak distracter: 4 pulses at 50 Hz).

Note that we chose this paradigm as the constant-current stimulators used in our setup did not allow for stimulus-by-stimulus modulation of intensity (i.e., distracters and targets in one trial/block were always of the same fixed intensity). Subjectively, an increase in pulse number gives a sensation of stronger stimulation (comparable with higher intensity stimuli). This distracter manipulation was effective, as the behavioral results indeed showed that discrimination rates were lower for the distracter conditions compared with the no-distracter condition.

A practice session was used to familiarize the subjects with the task. Subjects were seated upright in the magneto-encephalography (MEG) system and were instructed not to move during the experiment. After each set of 100 trials, subjects had a short break while they remained seated in the MEG system.

Data Acquisition

A whole-head MEG system with 275 axial gradiometers (CTF MEG Systems, Port Coquitlam, Canada) was used to record ongoing brain activity at a sampling frequency of 1200 Hz. The data were down-sampled off-line to 300 Hz. The subject's head location relative to the MEG sensors was measured at the start and end of each recording session using marker coils placed at the nasion and both ear canals.

In addition, anatomical MRIs of the subjects' brains were acquired using a 1.5-T Siemens Magnetom Sonata System (Erlangen, Germany). During MRI acquisition, similar earplugs, now with a drop of vitamin E in place of the coils, were used to allow coregistration of the MRI and MEG data for source analysis.

Data Analysis

Behavioral performance on the task was computed in terms of discrimination rate (percentage correct responses) and RT on correct trials. To assess the effect of conditions on performance, a repeated measures ANOVA with factor Distracter (no, weak, strong, and no*) was applied.

For the MEG data analysis, we used custom-built Matlab code and the Matlab-based FieldTrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011; http://www.ru.nl/neuroimaging/fieldtrip). For each subject, all trials were first cleaned from artifacts (this was done on all conditions combined). We used independent component analysis (Jung et al., 2000) to identify eye artifacts, which were then projected out of the data. Furthermore, trials with extremely high variance (containing, e.g., MEG sensor jumps or muscle artifacts) were removed from the data upon visual inspection (on average 6% of trials).

Sensor-level Analysis

Planar gradients of the MEG field distribution were calculated using a nearest-neighbor method (comparable with the method described by Bastiaansen & Knösche, 2000), which makes interpretation of the sensor-level data easier, as sensors showing maximal activity are typically located above the actual sources.

From each trial, the 1-sec prestimulus window ($t = 0.5$–1.5 sec) was extracted and multiplied with a Hanning taper, after which power spectra (4–36 Hz) were computed using a fast Fourier transform (FFT) approach. For the baseline contrasts (see below), power spectra were computed using the same approach, for a baseline ($t = -0.5$ to 0 sec) and prestimulus window ($t = 1$–1.5 sec). Note that here we used 0.5-sec long windows, as baseline length was limited to avoid bleeding in of effects of the previous trial (the intertrial interval was 1 sec).

Furthermore, time-frequency representations (TFRs) of power were computed to inspect the temporo-spectral pattern of power changes. We used an adaptive sliding time window of four cycles length ($\Delta t = 4/f$) for each frequency of interest, multiplied with a Hanning taper before estimating the power using an FFT approach.

Source Analysis

To disentangle contributions of somatosensory and posterior alpha sources, we applied a beamformer adaptive spatial filtering technique (Schoffelen, Oostenveld, & Fries, 2008; Gross et al., 2001). Using the individual ana-tomical MRI, we constructed a realistically shaped single-shell description of the brain for each subject. The brain volume was divided into a grid with a 1-cm resolution and normalized toward the template Montreal Neurological Institute (MNI) brain (International Consortium for Brain Mapping, Montreal Neurological Institute, Canada) using SPM8 (www.fil.ion.ucl.ac.uk/spm). Lead fields were calculated for all grid points (Nolte, 2003).

Fourier spectra (11 Hz) were obtained by applying a multitaper FFT approach to the 1-sec prestimulus segments, with five orthogonal Slepian tapers resulting in ±3 Hz smoothing (Percival & Walden, 1993), that is, a band of 8–14 Hz. With the lead fields and the Fourier spectra (of all conditions combined), a common spatial filter was constructed for each grid point, for each subject. Using this common filter, the spatial distribution of power was estimated for each trial separately. These power estimates were used for all reported analyses other than the baseline contrasts. For the baseline contrasts, source power estimates were computed using a similar common filter approach, now applied to the 0.5-sec baseline and prestimulus windows (note that the 0.5-sec window length was too short to use the same multitaper settings as described above, instead a Hanning taper, centered at 10 Hz, was applied).

The grid points ("voxels") included in the ROIs were selected on the basis of an anatomical atlas (Talairach & Tournoux, 1988). We used the following ROIs: left primary somatosensory cortex (centered at MNI coordinates [−50 −20 50], BA 3), right primary somatosensory cortex (MNI coordinates [50 −20 50]) and occipital cortex (MNI coordinates [−20 −80 30], including BA 7 and BA 17 and equivalent for the right hemisphere). A sphere of 30 grid points was placed centered at the coordinates provided by the atlas, and for each subject, power was averaged over grid points within each ROI.

Statistical Analysis

Statistical analysis was performed on the whole-brain source level alpha power. For each subject, trials were averaged for attention left and right separately and then contrasted the following way: (attention-left − attention-right)/(attention-left + attention-right). To establish whether the difference between attention left and right was significantly different from 0, a cluster-based nonparametric randomization test was applied within subjects (Maris & Oostenveld, 2007). By clustering neighboring grid points that show the same effect, this test deals with the multiple comparisons problem while taking into account the dependency of the data. For each grid point, a dependent samples t value was computed. All samples for which this t value exceeded an a priori threshold (uncorrected $p < .05$) were subsequently clustered on the basis of spatial adjacency. The sum of the t values within a cluster was used as cluster-level statistic, and the cluster with the maximum sum was used as test statistic. By randomizing the data across the two conditions (i.e., the normalized contrast and 0) and recalculating the

test statistic 2000 times, we obtained a reference distribution of maximum cluster t values to evaluate the statistic of the actual data.

Alpha Normalization

To assess the direction of the ipsilateral and contralateral effects, that is, to see if there was indeed an ipsilateral increase and contralateral decrease, we contrasted the prestimulus power ($t = 1–1.5$ sec) with precue baseline activity ($t = -0.5$ to 0 sec). For each subject, we baseline-normalized the single trial prestimulus alpha power in the following way: (prestimulus − avg-baseline)/avg-baseline, wherein avg-baseline is the mean baseline power over all trials and conditions in that subject (this was computed per sensor/grid point). This procedure reduces intersubject variability in the power estimates, thus providing a convenient normalization.

Next, to capture the modulation of ipsilateral and contralateral alpha power over conditions and its effect on behavioral performance, we normalized each single-trial prestimulus window ($t = 0.5–1.5$ sec) using the average prestimulus power over all trials and conditions in that subject. Hereby, we could separately address the contributions of ipsilateral and contralateral sides in a normalized measure (to exclude that subjects with particularly strong power values drive the result), while avoiding baseline effects to contribute to the observed effects. For each subject, we used the following normalization per trial: (prestimulus − avg-power)/avg-power, where avg-power is the average prestimulus alpha power for all trials combined, per subject.

RESULTS

MEG data were acquired while subjects performed a tactile stimulus discrimination task (Figure 1A), in which a visual cue directed attention either to their left or right hand. We manipulated the strength of distracters presented to the unattended hand.

Behavioral Performance

The average performance over all conditions in 24 subjects was 87.1 ± 8.8% correct responses and the mean RT was 526.4 ± 88.6 msec (computed on correct trials only). Figure 1B shows the average performance per condition. To assess the effect of the different conditions, a repeated measures ANOVA with factor Condition (no, weak, strong, and no* distracter) was performed. There was a significant effect of Condition both on discrimination rate ($F(3, 69) = 9.487, p < .001$) and RT ($F(3, 69) = 3.235, p < .05$). Post hoc pairwise comparisons showed that discrimination rate differed significantly between the no and weak distracter conditions (uncorrected $p < .01$), no versus strong ($p < .001$), no versus no* ($p < .001$) and weak versus strong ($p < .05$), and there was a trend for weak versus no* ($p = .1$). For RT, there was a significant difference between

the no and no* conditions (uncorrected $p < .05$), weak versus no* ($p < .05$), and a trend for strong versus no* ($p = .1$). To summarize, discrimination rate decreased as distracter strength increased, and in addition, performance decreased for the weak target condition.

Ipsilateral Increase and Contralateral Decrease of Alpha

Contrasting the prestimulus ($t = 0.5–1.5$ sec) alpha band power for attention to the left hand versus attention to the right hand, we confirmed our previous findings (Haegens, Händel, et al., 2011) and showed that the direction of attention is reflected in somatosensory alpha lateralization (Figure 2A; all conditions combined). Source reconstruction using a beamformer approach localized the bulk of the activity to the left and right primary somatosensory cortices (cluster-based randomization test $p < .01$; BA 3; Figure 2B).

Next, we asked whether the observed lateralization was caused by a contralateral decrease and/or ipsilateral increase versus baseline activity. It is crucial to do this analysis at the source level to disentangle somatosensory from posterior contributions (compare Figure 2A and B). The source reconstructions revealed an ipsilateral increase and a contralateral decrease versus baseline over somatosensory cortex (Figure 2B). Additionally, an increase of posterior alpha activity versus baseline can be observed. The differences between attention left and right were significant for both the left ($t(23) = 4.957, p < .001$) and right primary somatosensory cortex ($t(23) = -4.132, p < .001$), that is, somatosensory alpha activity was significantly lateralized (Figure 2C). A one-tailed t test of baseline-corrected contralateral alpha activity versus 0 was significant ($t(23) = -2.750, p < .01$), whereas ipsilateral alpha activity versus 0 showed only a trend ($t(23) = 1.104, p = .14$). Note that all trials (also incorrect responses) were included in this analysis and that the inter trial window was only 1 sec and thus rather short for return to a "stable" or "neutral" baseline. The crucial contrast to assess the relevance of the (ipsilateral) alpha modulation is correct versus incorrect trials (see below).

Furthermore, the TFR of power (Figure 2D) showed that the ipsilateral increase was limited to the alpha band and sustained throughout the prestimulus interval. While ipsilateral alpha increased, beta band activity (15–25 Hz) decreased, indicating a clear dissociation between the two rhythms. On the contralateral side, both alpha and beta band activity decreased versus baseline (not shown).

Thus, we report lateralization of alpha band activity, driven by both a contralateral decrease and, importantly, an ipsilateral increase of power. The sources of the lateralized alpha activity were localized to primary somatosensory cortex.

Alpha Power Influences Task Performance

To assess the influence of alpha power on task performance, we contrasted correct with incorrect response trials
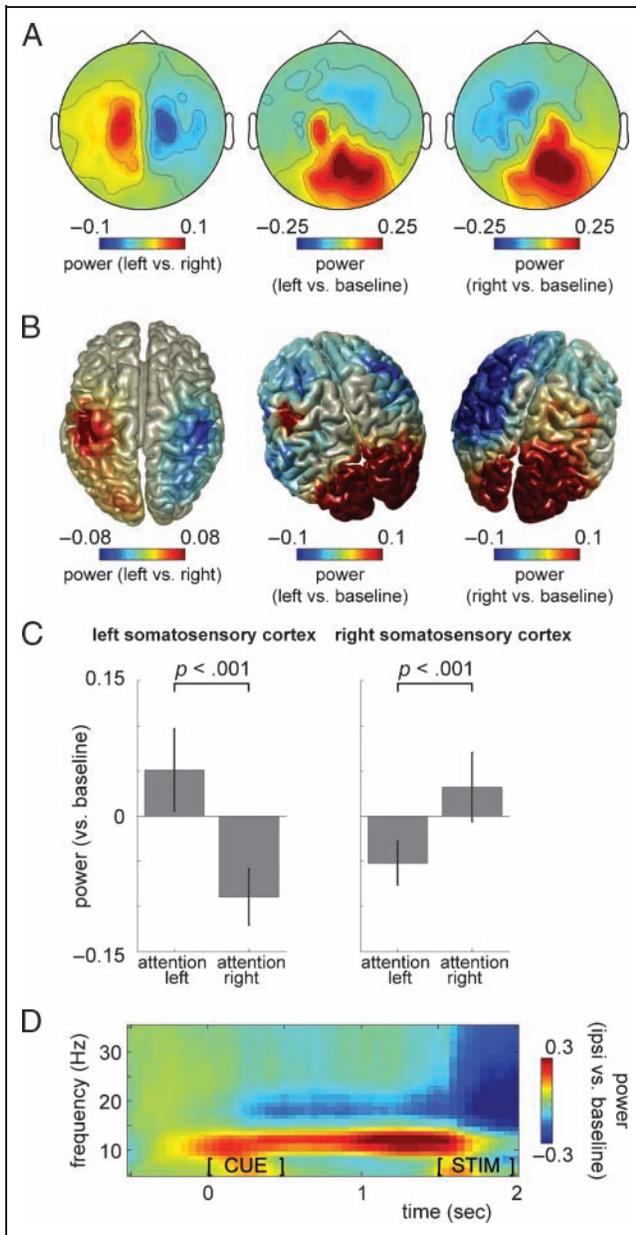
Figure 2. Prestimulus somatosensory alpha lateralization. (A) Topographic plots showing prestimulus alpha power (8–14 Hz) modulation in response to the cue (all conditions combined). Left: Attention left vs. attention right. Middle (right): Attention left (right) vs. baseline activity. All plots are showing data averaged over 24 subjects. (B) Alpha power source reconstructions obtained using beamformer technique, shown on a standardized brain volume. Peaks of the lateralized alpha activity are located in left and right primary somatosensory cortex (BA 3). Showing same contrasts as in A. (C) Bar graphs showing a significant ($p < .001$) ipsilateral increase versus contralateral decrease of alpha power for the somatosensory regions. Prestimulus alpha power was computed for each subject on the basis of the source level ROIs, normalized by the average baseline power in that subject. Error bars indicate *SEM*. (D) Average TFR of sensors over somatosensory regions, showing sustained increase of ipsilateral alpha activity during the prestimulus interval ($t = 0.5$–1.5 sec) compared with baseline ($t = -0.5$ to 0 sec). Left hemispheric sensors from the attention-left condition were combined with the right hemispheric sensors from the attention-right condition, "somatosensory" sensor selection on the basis of poststimulus response.

(all conditions combined). We found that correct trials had higher ipsilateral ($t(23) = 3.982, p < .001$) and lower contralateral alpha power ($t(23) = -2.100, p < .05$) than incorrect trials (Figure 3A). In addition, posterior alpha power was higher for correct than incorrect trials ($t(23) = 2.948, p < .01$). Note that, for this analysis, we combined all conditions to have a sufficient number of trials (especially the number of incorrect trials was low). However, further analysis confirmed that the effects went in the same direction (albeit not significant) when the individual conditions were considered (not shown).

We also compared trials with fast RTs versus slow RTs (median split). No significant differences were observed; there was a trend ($t(23) = 1.952, p = .06$) for fast RT trials having higher posterior alpha power than slow RT trials, however (Figure 3B).

These findings demonstrate that not only contralateral decrease but also ipsilateral increase of alpha is crucial for optimal performance. Thus, in addition to facilitation of stimulus processing, the blocking of potentially distracting input on the nonattended side plays a key role for discrimination performance.
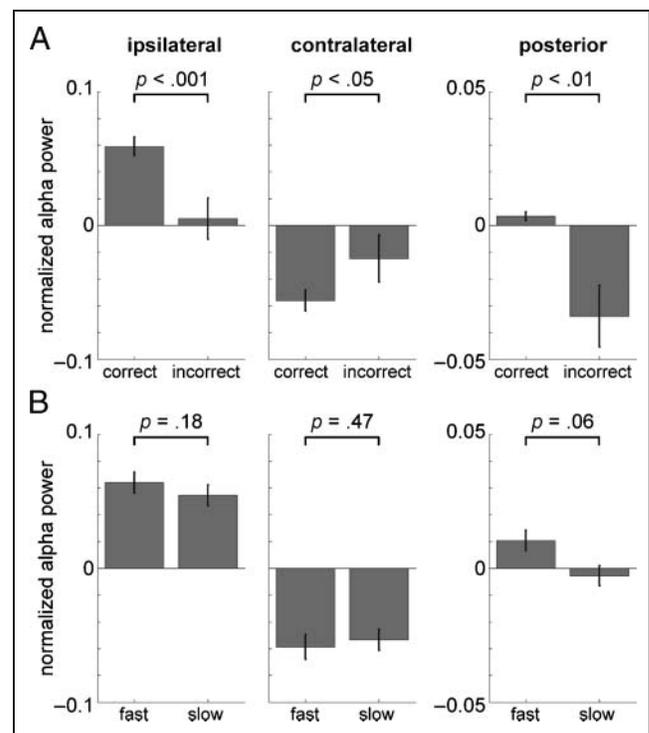

Figure 3. Prestimulus somatosensory alpha lateralization influences task performance. (A) Bar graphs showing significantly higher ipsilateral ($p < .001$), lower contralateral ($p < .05$) and higher posterior ($p < .01$) alpha power for correct compared with incorrect trials. Alpha power was computed for each subject on the basis of the source level ROIs, power for each trial was normalized by the average prestimulus alpha power in that subject. Error bars indicate *SEM*. (B) Similar graphs for fast versus slow RT trials. Here, the effects go in the same direction; however, they are not significant. A trend ($p = .06$) was observed for higher posterior alpha power for fast compared with slow RT trials.
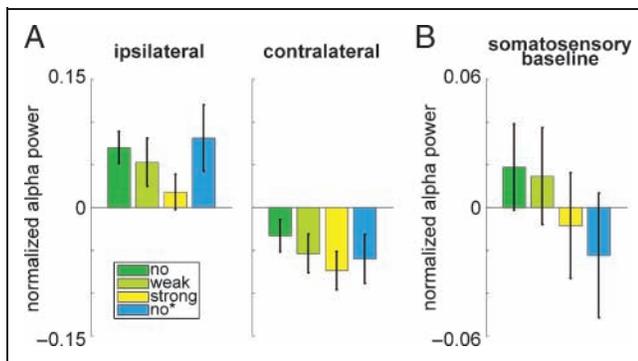
Figure 4. Effect of distracter strength. (A) Somatosensory alpha power decreased with increasing distracter strength, both for ipsilateral and contralateral alpha (statistical trend). Prestimulus alpha power was computed for each subject on the basis of the source level ROIs, power for each trial was normalized by the average prestimulus alpha power in that subject. Error bars indicate *SEM*. (B) Similar graph for the baseline alpha activity in the left and right somatosensory grid points combined.

Conditions

Next, we compared the somatosensory alpha power levels for the different distracter conditions. Here, we predicted that ipsilateral alpha power would increase with distracter strength whereas contralateral alpha power would either decrease or maintain the same level. Surprisingly, we found that alpha power decreased with conditions, for both the contralateral and the ipsilateral side (Figure 4A). Note that there was an ipsilateral increase versus baseline for all conditions (not shown); with "decrease," we here refer to relative changes between conditions. Given a substantial variance between subjects, these decreases only reflected statistical trends (comparing no vs. strong distracter condition, for ipsilateral: $t(23) = 1.760$, $p = .09$; and for contralateral: $t(23) = 1.438$, $p = .16$; all other comparisons not significant). A two-way ANOVA with factors Hemisphere (ipsilateral vs. contralateral) and Condition (no, weak, strong) showed only a significant effect of Hemisphere ($F(1, 23) = 48.959$, $p < .001$). The factor Condition was not significant ($F(2, 46) = 1.176$, $p = .32$), and there was no significant interaction of Hemisphere × Condition ($F(2, 46) = 0.628$, $p = .54$). Upon inspection of the baseline alpha levels, it turned out that already baseline power levels revealed a (although not significant) decrease over conditions (Figure 4B).

Contrary to our predictions, we found a weak decrease (statistical trend) of both contralateral and ipsilateral alpha activity with increasing distracter strength. These patterns are unlikely to be caused by the (evoked) response to the distracters carrying over into baseline/prestimulus windows, as we see a similar pattern for the baseline alpha in the no* condition. Furthermore, there was a significant effect of Condition on performance, with discrimination rates decreasing with increasing distracter strength. These behavioral effects imply that indeed the task with stronger distracters was more difficult hence requiring more effort

(and perhaps alertness). A possible explanation could be that with increasing task difficulty, vigilance increases, which then is reflected in a more general alpha power decrease.

Context Effect

Unexpectedly, we found ipsilateral alpha power to increase compared with baseline activity in all conditions, even in the ones without distracters (the no and no* conditions). This is in contrast to our previous study on somatosensory spatial attention, in which we reported somatosensory alpha lateralization that was mainly driven by a contralateral decrease in alpha power. There, we showed that somatosensory alpha lateralization is under flexible top–down control: subjects were able to use information about cue reliability and adapt their attention accordingly. The reliability of the cue was varied in three experimental blocks (100%, 75%, or 50% valid cueing) and alpha lateralization levels increased with increasing cue reliability. Note that, despite the presence of weak distracters, in our previous study we did not observe a systematic ipsilateral increase of alpha, possibly because the rather weak distracters did not require active suppression (Haegens, Händel, et al., 2011). To shed further light on this difference, we directly compared the results from the previous with the current study. We computed the ipsilateral and contralateral alpha power versus baseline for the no-distracter condition of the current study (Figure 5A) and performed the same analysis on the 100% cue-reliability condition of our previous study (see Haegens, Händel, et al., 2011) on source level using the same ROIs (Figure 5B).
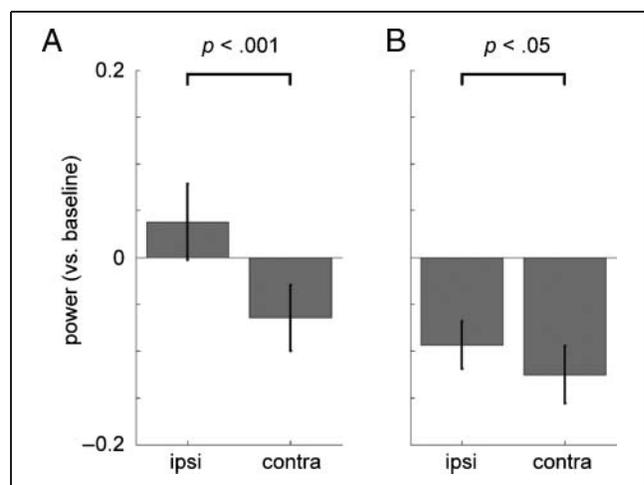

Figure 5. Context effect. Comparison of ipsilateral and contralateral prestimulus alpha power versus baseline for the current study (A; no-distracter condition) and our previous study (B; 100% cue-reliability condition) as described in Haegens, Händel, et al. (2011). Prestimulus alpha power was computed for each subject on the basis of the source level ROIs, normalized by the average baseline power in that subject. Error bars indicate *SEM*.

To directly compare the two studies, we computed a two-way mixed ANOVA with factors Study (current vs. previous; between-subject factor) and Hemisphere (ipsilateral vs. contralateral; repeated measures factor). There was a significant main effect of Hemisphere, confirming a difference between ipsi- and contralateral alpha levels ($F(1, 39) = 24.071, p < .001$), that is, alpha lateralization. The between-group factor Study was near significance ($F(1, 39) = 3.809, p = .058$). Importantly, there was a significant interaction effect between Hemisphere and Study ($F(1, 39) = 6.643, p < .05$). Although in both studies we report a significant difference between ipsilateral and contralateral modulation (current: $t(23) = 4.862, p < .001$; previous: $t(16) = 2.456, p < .05$), different strategies were adopted. Clearly, the introduction of distracters in the current study led to a pattern of ipsilateral alpha increase (vs. baseline), even in the no-distracter conditions, whereas in the previous study a decrease was reported.

DISCUSSION

In the current study, we tested the hypothesis that an increase of alpha band activity serves to suppress task-irrelevant, distracting input. We used a somatosensory spatial attention task where subjects had to discriminate stimuli presented to the cued hand while distracters were presented to the non-attended side. We show that the anticipation of distracters indeed leads to an ipsilateral alpha increase, in addition to a contralateral decrease and a general posterior alpha increase. Using source level analysis—crucial to disentangle the primary somatosensory and posterior contributions—we were able to show that these three alpha components all contributed to optimal task performance. Importantly, not only contralateral decrease but also ipsilateral increase of alpha activity plays a key role in predicting discrimination performance.

The current findings are in line with our previous work showing that somatosensory alpha influences discrimination performance (Haegens, Händel, et al., 2011; Haegens, Osipova, Oostenveld, & Jensen, 2010), and with the visuospatial attention literature (Rihs et al., 2009; Kelly et al., 2006; Thut et al., 2006; Fu et al., 2001; Worden et al., 2000; Foxe et al., 1998). Altogether, this provides further evidence that rolandic/somatosensory alpha and posterior/visual alpha activity play similar roles for the respective sensory systems (Ritter, Moosmann, & Villringer, 2009), thereby strengthening the case that alpha activity reflects a general mechanism for functional engagement and disengagement (Jensen & Mazaheri, 2010; Klimesch et al., 2007; Cooper et al., 2003). Here, we show that alpha activity is crucial not only for facilitation of processing on the attended side but also in the blocking of potentially distracting input on the nonattended side.

Alpha Modulation Depends on Task Context

Interestingly, whereas in our previous spatial attention study alpha lateralization seemed to be mainly driven by a decrease contralateral to the attended side (Haegens, Händel, et al., 2011), we now report an additional ipsilateral increase, even in the blocks with no distracter present. Although we did hypothesize alpha increase to be dependent on task requirements, it is striking that the increase is observed even in the conditions where there is seemingly no requirement for suppression. A possible explanation is that the persistent ipsilateral increase reflects a context effect. Subjects were trained on all conditions before the experimental recordings, and conditions were presented in a random order. Hence, it is possible that subjects adopt a strategy which includes both facilitation of the attended side and suppression of the unattended side and use this same strategy throughout the experiment, rather than just on the distracter blocks. Our finding is in line with previous work on selective visuospatial attention also reporting alpha increase in the absence of distracters, which the authors ascribe to task demand and context (Rihs et al., 2007, 2009).

Vigilance Reflected by Alpha Decrease?

Manipulating the distracter strength in four experimental conditions (no, weak, and strong distracter, and a fourth condition with no distracter but weaker stimulus to control for task difficulty independent of distracter presence) led to some unexpected results. Although we predicted a further increase of ipsilateral alpha with increasing distracter load, potentially accompanied by a contralateral decrease, we observed a general decrease of alpha activity in both the contralateral and ipsilateral hemispheres with increasing task difficulty (statistical trend only; note that with "decrease," we here refer to relative decreases comparing conditions, for all conditions ipsilateral alpha activity increased relative to the baseline). Upon further inspection, it turned out that already baseline levels of alpha showed a weak negative modulation.

These findings are in contrast with a study on visual working memory by Sauseng et al. (2009), showing an increase of ipsilateral posterior alpha with increase of distracter load, which predicted individual memory capacity. The global decrease of alpha level with increasing distracter level we find here might be reflecting an increase in vigilance or arousal because of increasing task demands (Bollimunta, Mo, Schroeder, & Ding, 2011; Klimesch et al., 2007; Pfurtscheller & Lopes da Silva, 1999; Ray & Cole, 1985). This interpretation would be in line with previous work showing that spontaneous fluctuations in ongoing alpha activity reflect changes in detection ability of near-threshold stimuli, with lower alpha levels related to better perceptual performance (Hanslmayr, Gross, Klimesch, & Shapiro, 2011; Zhang & Ding, 2010; Hanslmayr et al., 2007; Ergenoglu et al., 2004; Linkenkaer-Hansen, Nikulin, Palva, Ilmoniemi, & Palva, 2004).

Given the spatial resolution of the currently used methods, it is hard to tell whether on top of this global alpha decrease there was still a modulation of ipsilateral

alpha. Previous studies have suggested a "center-surround" pattern of alpha modulation for directing focal attention (Suffczynski, Kalitzin, Pfurtscheller, & Lopes da Silva, 2001; Pfurtscheller & Lopes da Silva, 1999). We might be tapping into a similar mechanism here, and perhaps the MEG/beamformer approach is not spatially sensitive enough to detect such a focal effect. Alternatively, it could be that the alpha increase plateaus at a certain level and further increases do not lead to any additional benefits.

Alpha versus Beta Activity

Previous work on somatosensory attention has reported that—in addition to alpha—beta band activity predicts detection performance (Schubert, Haufe, Blankenburg, Villringer, & Curio, 2009) and is modulated by expectation (Van Ede et al., 2011; Van Ede, Jensen, & Maris, 2010), suggesting that somatosensory alpha and beta activity reflect similar or related mechanisms (although there is an ongoing debate as to whether these rhythms originate from the same sources, see, e.g., Van Ede et al., 2010; Cheyne et al., 2003; Hari & Salmelin, 1997). However, here we report a dissociation between alpha and beta band responses, as the ipsilateral alpha increase was accompanied by a beta band decrease (Figure 2D). Furthermore, beta band oscillations have been implicated in somatosensory working memory maintenance and decision-making (Haegens, Nácher, et al., 2011; Spitzer & Blankenburg, 2011; Spitzer, Wacker, & Blankenburg, 2010). It seems that alpha is generally reflective of the state of the sensory system, whereas beta plays a more versatile role and is perhaps also involved in active processing.

Conclusion

Our findings demonstrate that alpha power is modulated depending on task demands: Contralateral alpha activity decreases when the main requirement is stimulus detection, whereas ipsilateral alpha activity increases when active suppression of distracters is important. Both contralateral and ipsilateral alpha modulations are required for optimal task performance. This study further extends the notion that alpha band activity is involved in shaping the functional architecture of the working brain by determining the engagement and disengagement of specific regions.

Our study prompts the following questions to be addressed in the future: Clearly the alpha activity in somatosensory and visual regions is under strong top–down control; which regions and mechanisms control the alpha activity? The alpha activity is likely to exercise gain control by modulating the spikes encoding the sensory representations; what is the underlying mechanism by which alpha oscillations modulate the spike activity? Further research, including intracranial (spike) recordings, is required to address these issues.

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