

## ATTENTIONAL MODULATION OF THE SOMATOSENSORY MU RHYTHM

K. L. ANDERSON AND M. DING\*

The J. Crayton Pruitt Family Department of Biomedical Engineering,  
University of Florida, Gainesville, FL 32611, USA

**Abstract**—Neural oscillations with a frequency of around 10 Hz are thought to be a ubiquitous phenomenon in sensory cortices, and it has been hypothesized that the level of 10 Hz activity is related to local cortical excitability. During spatial attention, the visual alpha rhythm has been found to be modulated according to the direction of attention. Specifically, the alpha rhythm desynchronizes over visual cortex contralateral to the direction of attention and synchronizes over visual cortex ipsilateral to the direction of attention, and these modulations have been associated with facilitation and inhibition of sensory processing. In the somatosensory domain, the reactivity of a similar rhythm, known as the mu rhythm, during attention tasks is a current topic of inquiry and somatotopic modulation of the mu rhythm by directed attention have been reported. In this paper, we investigate how lateralized spatial attention modulates the ongoing somatosensory mu rhythm, and how such modulation impacts sensory information processing. 128 channel EEG was recorded while subjects performed a somatosensory spatial attention task. In addition to analyses on scalp recorded data, a spatial filtering method was utilized to investigate spatial attention effects in the source space. The direction of spatial attention was found to have a significant somatotopic effect on the ongoing mu rhythm occurring in primary somatosensory cortex. Concurrently, the visual alpha rhythm was significantly elevated above the baseline level during somatosensory attention, demonstrating a cross-modal effect. Lastly, an analysis was performed to investigate the correlation between the level of prestimulus mu activity and subsequent stimulus evoked activity in primary somatosensory cortex. © 2011 IBRO. Published by Elsevier Ltd. All rights reserved.

**Key words:** EEG, somatosensory, neural oscillations, Mu, alpha, ERPs.

Field oscillations in the 8–12 Hz range have been observed in visual, somatosensory, and auditory cortices, and they are referred to as alpha, mu, and tau rhythms, respectively. Among these rhythms, visual alpha is the most extensively studied (Shaw, 2003). Typically, the amplitude of alpha is higher over visual areas that are not engaged in a task and lower over areas that are engaged. In particular, when attention is deployed to a location in

visual space, decreased alpha amplitudes (desynchronization) have been found over visual areas contralateral to the direction of attention (Sauseng et al., 2005; Thut et al., 2006; Wyart and Tallon-Baudry, 2008), a modulation which is thought to reflect the engagement of relevant cortical areas (Medendorp et al., 2007) through a local increase of cortical excitability (Klimesch et al., 2007; Romei et al., 2008; Worden et al., 2000). Conversely, an increase in alpha amplitude, known as synchronization, has been reported over visual cortex ipsilateral to the attended direction (Kelly et al., 2006; Rihs et al., 2007; Worden et al., 2000; Yamagishi et al., 2003). This increase is considered by some to reflect a “gating” mechanism, whereby processing of irrelevant stimuli is inhibited in order to better process relevant stimuli (Cooper et al., 2003; Jensen et al., 2002; Klimesch et al., 2007). It has been shown that alpha synchronization and desynchronization also play an important role in other high-order cognitive processes such as memory and visual imagery (Jensen et al., 2002; Klimesch et al., 1999; Medendorp et al., 2007; Tuladhar et al., 2007).

Are these functional properties of visual alpha shared by similar oscillations in other sensory cortices? The mu rhythm over somatosensory cortex (Gastaut, 1952) is known to behave similarly to the visual alpha rhythm in some respects. For example, a decrease in amplitude of mu, known as an event related desynchronization (ERD), has been noted following somatosensory stimulation (Pfurtscheller, 1989; Nikouline et al., 2000a; Della Penna et al., 2004), which is akin to the parieto-occipital alpha ERD that occurs after visual stimulation (Pfurtscheller et al., 1979, 1994; Vijn et al., 1991). As another example, alpha rhythms overlying dorsal stream (“where” pathway) areas have been found to increase in amplitude during a visual working memory task that engages the ventral stream (“what” pathway) (Jokisch and Jensen, 2007). A similar effect has been seen during a somatosensory delayed-match-to-sample task, where mu power was higher over areas hypothesized to be not engaged by the task, such as somatosensory cortex ipsilateral to the sample stimulus (Haegens et al., 2010).

Despite these similarities, whether and how the ongoing somatosensory mu rhythm responds topographically to spatial attention, a hallmark of visual alpha reactivity, has only recently been investigated. Jones et al. (2010), using magnetoencephalography (MEG), found that cued spatial attention to the hand decreased mu power in the hand area of primary somatosensory cortex (SI) while attention to the foot on the same side of the body was accompanied by a mu power increase in the hand area. Also utilizing MEG, van Ede et al. (2010) found that attentive as well as non-

\*Corresponding author. Tel: +1-352-392-0354; fax: +1-352-392-9791.

E-mail address: mingzhou.ding@bme.ufl.edu (M. Ding).

**Abbreviations:** BOLD, blood oxygenation level-dependent; ERD, event related desynchronization; ERP, event related potential; fMRI, functional magnetic resonance imaging; LF, lateral-frontal; MEG, magnetoencephalography; MF, medial frontal; O, occipital; PP, posterior parietal; PSDs, power spectral densities; SI, primary somatosensory cortex; SII, secondary somatosensory cortex.

0306-4522/11 \$ - see front matter © 2011 IBRO. Published by Elsevier Ltd. All rights reserved.

doi:10.1016/j.neuroscience.2011.02.004

attentive expectation of a somatosensory stimulus modulated, in a lateralized manner, the beta rhythm, a 15–35 Hz somatomotor rhythm with some functional similarities to the mu rhythm (Salenius et al., 1997; Pfurtscheller and Lopes da Silva, 1999; Ritter et al., 2009). No such expectation effect was seen for the mu rhythm. While in the MEG modality, beta-band activity is often analyzed along with or in lieu of mu activity (Jones et al., 2009, 2010; van Ede et al., 2010), the beta rhythm is often not very prominent in EEG recordings (Zhang and Ding, 2010).

The effect of lateralized spatial attention on the somatosensory mu rhythm currently remains uninvestigated. We recorded high-density EEG while subjects performed a somatosensory spatial attention task in which sustained attention was directed to either the right or the left hand. Oscillatory activity in the 8–12 Hz (mu) and 15–35 Hz (beta) frequency range during a prestimulus time period when somatosensory attention was deployed to either direction was measured and compared with a baseline period. A spatial filter was applied to the scalp-recorded data in order to investigate the effects of somatosensory spatial attention on cortical areas such as SI, secondary somatosensory cortex (SII), posterior parietal cortex, lateral and medial frontal areas, and occipital cortex. The inclusion of the occipital cortex (a) removed a potential source of volume conduction that might negatively impact the estimation of somatosensory mu activity which is smaller in magnitude than visual alpha and (b) allowed the examination of possible cross-modal attention effects. Finally, the effect of the mu rhythm prior to stimulus onset on stimulus processing during different states of attention was investigated by correlating prestimulus mu power with evoked activity in SI. Although the relationship between prestimulus mu power and evoked potentials has been investigated previously (Nikouline et al., 2000b; Jones et al., 2009, 2010; Reinacher et al., 2009; Zhang and Ding, 2010), the current analyses extend these findings by revealing the impact of source-localized estimates of high, low, and intermediate amplitudes of prestimulus mu on early and late evoked activity during different attentional states.

## EXPERIMENTAL PROCEDURES

### Participants

A total of 15 healthy right-handed subjects (aged 19–27 years, eight female) participated in the experiment. All participants pro-

vided written informed consent and were paid in accordance with the guidelines of the Institutional Review Board (IRB-02) at the University of Florida. All subjects performed the task according to instructions and were included in the following analyses.

### Stimulation device

Somatosensory stimuli were delivered using a two-channel, custom built, computer controlled, constant-current stimulation device. The device was optically isolated from the stimulus presentation computer and battery powered to ensure the participant's safety and that no additional line noise was introduced into the recording. Stimulus amplitude was adjustable from 0 to 5 mA in ~0.02 mA steps and stimulus duration was fixed at 0.5 ms. Event triggers sent to the EEG recording amplifier were precise to the sub-millisecond level.

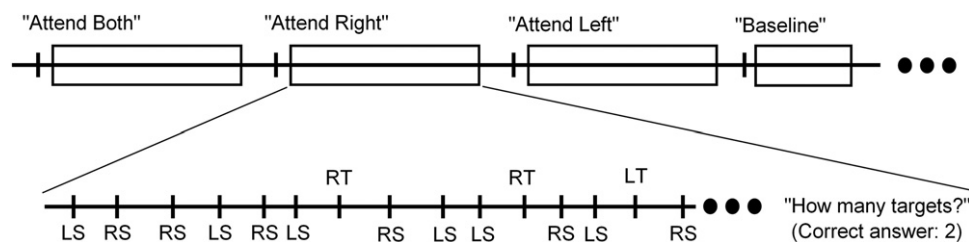
### EEG recording

The experiment took place in a dimly-lit, acoustically and electrically shielded booth. Subjects sat comfortably in a chair with their arms apart and resting on a table in front of them. They were instructed to keep their eyes open and fixated on a small cross on a computer monitor 1.5 m in front of them throughout the experiment.

The EEG data were acquired using a 128-channel BioSemi ActiveTwo System ([www.biosemi.com](http://www.biosemi.com)) with a sampling rate of 2048 Hz. Four channels of electrooculogram (EOG) were recorded in addition to the 128 scalp channels. Statistical analyses of scalp-recorded data were performed on electrodes CP3 and CP4. These electrodes were chosen to represent activity over primary somatosensory cortex because they are where the largest early (~50 ms post-stimulus) evoked activity was measured.

### Experimental design and paradigm

The task was a somatosensory oddball task involving directed spatial attention. A block design was used. Subjects were instructed to fixate on a cross in the center of a computer screen and direct their attention to either their right (attend-right or ATTR), left (attend-left or ATTL), or both (attend-both or ATTB) hands during a block (Fig. 1). Each block consisted of 70 electrical stimuli being delivered over either the right or left median nerve with equal probability. The inter-stimulus interval was uniformly distributed between 2.5 and 3.5 s. Each stimulus could either be a standard (low amplitude, 80–92% probability) or a target (higher amplitude, 8–20% probability). The amplitude of the standard stimulus was held fixed throughout the experiment at twice the detection threshold for each hand. Here, the detection threshold for each hand was determined using an up-down staircase procedure (Leek, 2001) to find the amplitude at which the subject detected the stimulus 50% of the time. Amplitudes for the target stimuli were initially set during a short practice run before the experiment to achieve a target detection error rate of around 25% for both the



**Fig. 1.** Schematic of the experimental paradigm. The top section illustrates three experimental blocks and a baseline period. The subject is instructed before each block which hand to attend to. The lower section illustrates the stimulus sequence in an experimental block. Abbreviations for stimuli are: LS, left standard; RS, right standard; LT, left target; RT, right target. Stimuli are randomly delivered to the left and right median nerves with interstimulus intervals of between 2.5 and 3.5 s. Subjects are instructed to mentally count the number of target stimuli to the attended hand(s). At the end of each block, subjects are asked to report the number of targets detected.

attend-left and attend-right conditions. During the experiment, target amplitudes were adjusted at every third block to keep the error rate for the attend-left and attend-right conditions around 25%. As the target stimuli were not held constant throughout the experiment, only data from standard stimuli were used for the analyses in this paper.

Before each block, the subjects were instructed to mentally count the number of target stimuli delivered to the attended hand and to ignore stimuli delivered to the unattended hand. In the attend-both condition, the subjects were instructed to count the total number of targets delivered to both hands. The subjects verbally reported the number of detected targets at the end of each block. A fourth, baseline, condition without any stimuli was recorded at the beginning of the experiment and every six blocks, in which the subject was instructed to relax and stare at the fixation cross (as in the other blocks) for 3 min. The order of the blocks, in groups of three, alternated between ATTB → ATTR → ATTL and ATTB → ATTL → ATTR. In total, the experiment consisted of between 15 and 18 blocks of stimuli (five to six each of ATTB, ATTR, ATTL) and three to four baseline blocks, resulting in 175–210 stimuli per-condition, per-hand (1050–1260 total). For the current study, only the attend-left, attend-right, and baseline conditions were analyzed.

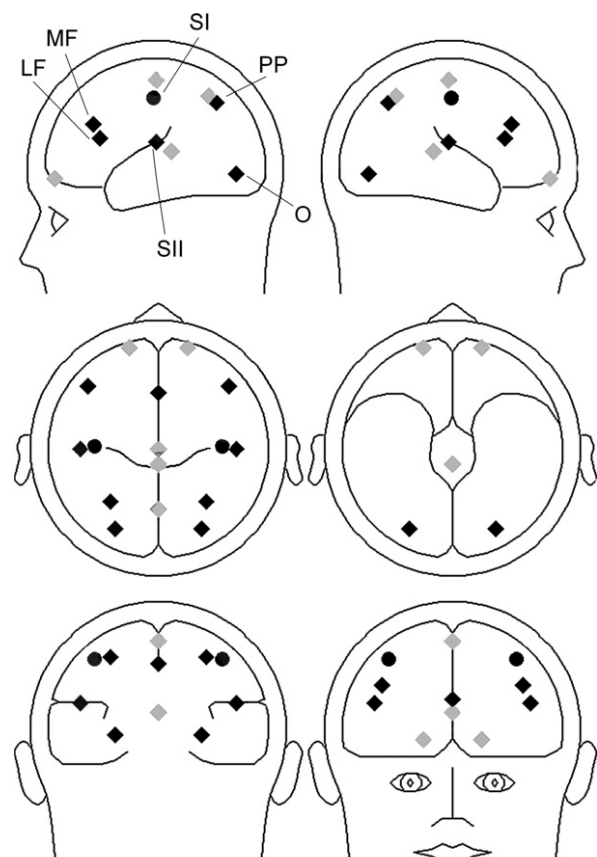
### Source estimation

Electrode locations, as well as three fiducial landmarks, were digitized by means of a Polhemus spatial digitizer. Regional dipole source analysis (Scherg, 1992) was used to create a spatial filter using the Brain Electrical Source Analysis (BESA) software package which implements a least squares algorithm to solve the overdetermined problem and estimate the activity contributed by each source to the scalp-recorded data. Based on findings from previous research, relevant fixed regional sources were seeded into a four-shell ellipsoidal head model (brain, cerebrospinal fluid, skull, and skin conductivities of .33, 1.0, .0042, and .33 mohm/m, respectively) and source activity was estimated from each subject's continuous scalp data for further analyses.

As illustrated in Fig. 2, 11 sources were seeded in relevant brain areas:

- Bilateral primary somatosensory (SI) sources were seeded near the postcentral gyrus, consistent with the hand area found in previous studies (Bowsher et al., 2004; Della Penna et al., 2004; Gaetz and Cheyne, 2006; Ritter et al., 2009; Valeriani et al., 1997; Waberski et al., 2002).
- Bilateral secondary somatosensory (SII) sources were seeded near the parietal operculum. Coordinates were chosen based on a meta-analysis (Eickhoff et al., 2006).
- Bilateral posterior parietal (PP) sources were seeded near the superior parietal lobule, a location indicated as being involved in maintaining spatial attention (Corbetta et al., 1998; Kastner and Ungerleider, 2000).
- Bilateral lateral-frontal (LF) sources were seeded near the middle frontal gyrus. Source sensitivity maps (not shown) for these dipoles indicated contributions from both dorsolateral prefrontal cortex and frontal eye fields.
- A medial frontal source (MF) was seeded near the inter-hemispheric space between the left and right anterior cingulate gyri.
- Bilateral occipital (O) sources were seeded near the foveal confluence, an area where V1, V2, and V3 are thought to converge (Dougherty et al., 2003; Schira et al., 2009).

In addition to the above 11 task-relevant sources, five more sources were seeded to minimize contamination of estimated source activity from other brain areas.



Source ID	Brodman Area (Approx)	Description	X	Y	Z
SI	3,1,2	Postcentral Gyrus (Hand Area)	+/- 40	-21	+48
SII	40	Parietal Operculum	+/- 49	-19	+18
PP	7	Superior Parietal Lobule	+/- 30	-65	+45
LF	9	Middle Frontal Gyrus	+/- 44	+29	+35
MF	33	Anterior Cingulate	+0	+25	+25
O	18,19	Visual Cortex	+/- 27	-79	-10
FP	10,11	Frontal Pole	+/- 18	+64	+1
CM	-	Central Midline	+0	-25	+60
PM	-	Parietal Midline	+0	-70	+40
D	-	Deep Midline	+0	-30	+10

Fig. 2. Regional sources seeded for source space analysis. Coordinates for the sources are in Talairach space. The 11 sources analyzed in this study are in black and labeled in the upper-left schematic.

- Bilateral sources were seeded near the frontal poles. These sources were used to account for ocular activity that was below the rejection threshold.
- Central and parietal midline sources were seeded to minimize lateral source sensitivity overlap.
- A deep midline source was seeded to account for additional brain activity. The source sensitivity map (not shown) indicated mostly local (subcortical) and inferior temporal lobe contributions to this source.

For each of the 16 regional sources seeded, magnitudes of ERPs and spectral estimates of ongoing neuronal activities from the three dipolar components were used to obtain orientation-independent measures. Note that, as no structural images were obtained from the participants, source locations should be considered approximate. However, estimated source waveforms are relatively insensitive to variations in dipole location.



## Data preprocessing

Two sets of data, sensor-level and source-level, were analyzed in this study. Preprocessing steps were similar for both data sets, and any differences will be noted below.

As the exact locations of the recording electrodes were slightly different for each subject, spherical spline interpolation was used to transform each subject's 128+4 channels of data into a standard 81-channel 10–10 montage. This spatially interpolated data set was used for all sensor-level analyses. Channels with poor signal quality for each individual subject were not included in this transformation. All sensor-level analyses were performed on the average referenced data.

First, the signals were band-pass filtered between 0.3 and 85 Hz and down-sampled to 256 Hz for subsequent analyses. The data were then epoched around each standard stimulus from –700 ms to 500 ms. For baseline data, artificial triggers were inserted into the continuous recordings every 600 to 800 ms, and epoched as above (note that only the "prestimulus" period from –500 ms to 0 ms, with 0 ms denoting the onset of an artificial trigger, was used for baseline analyses). After this, the DC component was subtracted from each epoch. Any epoch with activity in the EOG channels exceeding 75  $\mu\text{V}$ , or with activity exceeding 50  $\mu\text{V}$  in any scalp channel, was excluded from further analysis. This procedure resulted in between ~15% to ~30% of epochs being rejected from each subject.

## Behavior and evoked potential analysis

Behavioral performance for each block was measured as (targets reported – actual targets)/(actual targets). The amplitude of target stimuli was adjusted throughout the experiment to obtain consistent behavioral results.

The mean of the prestimulus baseline period from –100 to 0 ms was subtracted from each epoch before averaging. The ERPs for each subject were weighted equally to compute the grand average. The source space ERPs were computed as the square root of the sum of each of the three dipole components squared. A Wilcoxon signed-rank test was used at each time point to test whether the difference between conditions was statistically significant. If the tests on at least three consecutive sample points (~12 ms) resulted in *P*-values less than 0.05, the effect in that time period was considered significant.

## Spectral power analyses

Spectral power analyses were performed on a time period immediately preceding all artifact-free standard stimuli in the attend-right and attend-left conditions. For the baseline condition, the analyses were performed on the same time window preceding the artificially inserted triggers described in "Data preprocessing". This time window was defined to be from –500 ms to 0 ms relative to each stimulus/trigger. This prestimulus window was chosen to be short enough as to minimize the effect of the neuronal response to the previous stimulus and to capture a stable state of the brain at the time of stimulus onset while at the same time long enough to allow for sufficient frequency resolution. For all channels and source dipoles, power spectral densities (PSDs) were estimated for each prestimulus epoch using a multitaper Fast Fourier Transform (FFT) approach with three Discrete Prolate Spheroidal Sequence (DPSS) tapers over this time window, resulting in  $\pm 4$  Hz smoothing. In order to obtain an orientation-independent measure in the source space, magnitudes of the PSDs for each source at each epoch were obtained by taking the square root of the sum of the squares of each dipole component's PSD. When plotting power spectra (Figs. 4 and 5), spline interpolation was used to obtain a more smooth curve.

We used the estimated spectral power between 8 and 12 Hz to compute the average mu band power and 15 to 35 Hz to

compute the average beta band power. To facilitate averaging across subjects, the average band power was normalized by finding the ratio between the power of each condition and the mean power of all three conditions for that subject. As an example, the normalized band power for the *ignore* condition in a single subject would be calculated as: (ignore)/(ignore+attend+baseline)/3. A Wilcoxon signed-rank test was used to test whether the difference between two conditions was statistically significant.

## Correlation between prestimulus mu power and evoked potential amplitude

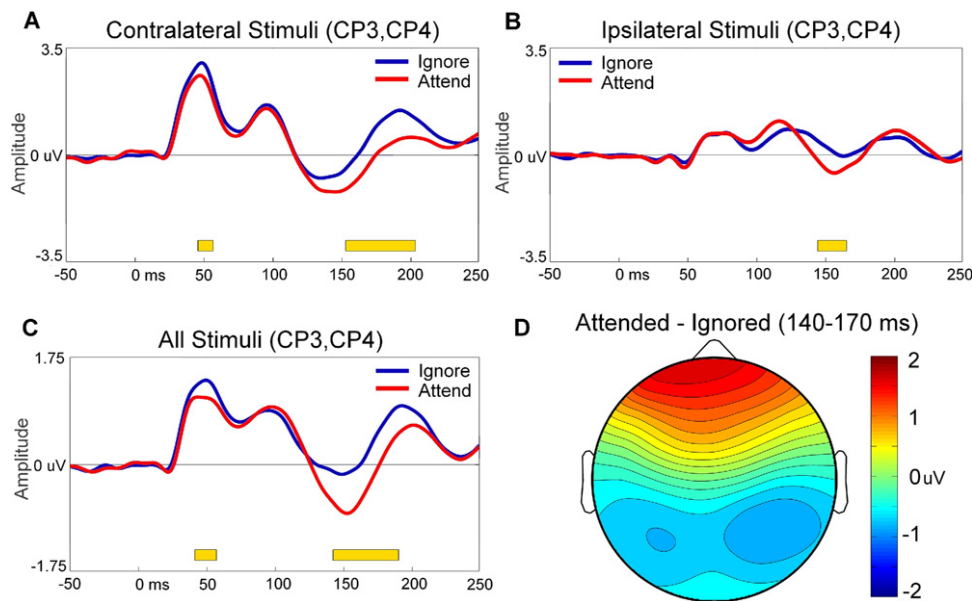
To analyze the correlation between prestimulus mu power and evoked potential amplitude in SI, trials for each subject and each condition were divided into two groups: right stimuli and left stimuli. The trials in each group were then rank ordered by the amplitude of the prestimulus mu power estimated from the SI source contralateral to stimulation, and sorted into five bins of equal size with an overlap of 50%. Each bin contained about 33% of the total available trials in each group. The power bins were indexed from 1 to 5 where Bin 1 has the smallest mu power and Bin 5 has the largest.

For each subject, the trials within a power bin were used to calculate the evoked activity in source SI in the same way as described in the above section on behavior and evoked potential analysis. The mean amplitudes of the evoked activity in two time ranges: 45–55 ms and 140–160 ms, centered on the peaks of evoked activity in the SI source, and where significant differences between the amplitudes of the sensor-level somatosensory evoked potential (SEP) were found, were then computed for each bin. To minimize the effect of inter-subject variability in evoked activity amplitude on population averaging, the following procedure was adopted to normalize the data from each subject. Let the mean amplitude for Subject *K* in Power Bin *J* be denoted as  $A(K,J)$ . The mean evoked amplitude for this subject will be calculated as  $\text{mean}_A(K) = [A(K,1) + A(K,2) + \dots + A(K,5)]/5$ . The normalized evoked amplitude was calculated as the percent change against this mean, namely,  $\text{norm}_A(K,J) = (A(K,J) - \text{mean}_A(K)) / \text{mean}_A(K)$ . This normalized evoked amplitude was then averaged across subjects to obtain the mean normalized evoked amplitude for each power bin. The results were then combined across hemispheres. For the early evoked component (45–55 ms), Spearman's rank correlation coefficients were computed to test for statistical dependence. A quadratic regression was performed on the late component (140–160 ms).

Similar analyses were performed on the other bilateral sources (SII, PP, LF, and O). For each source, the time intervals chosen for analysis were defined according to where a significant difference was found between the grand average evoked activity to attended and unattended contralateral somatosensory stimuli.

## Time frequency analysis of mu and beta activity in SI

The temporal evolution of mu and beta power was compared between different attention conditions for the SI sources. First, the data were epoched from –1500 to 2500 ms around each standard stimulus or, for the baseline condition, each artificially inserted trigger (see Data preprocessing). Epochs containing artifacts during this time period were rejected from further analysis. The data from each epoch were then time-frequency decomposed by convolving with Morlet wavelets to obtain power estimates from 8–12 Hz and 15–35 Hz with center frequencies at 1 Hz intervals. The time course of the mean band power was then calculated for each trial and averaged within each condition. As with the prestimulus power analysis described in "Spectral power analyses", an orientation-independent measure was obtained by calculating the magnitude of the power estimates from the three dipoles in each regional source for each time point. Results were then combined across hemispheres in a way similar to that described in "Spectral



**Fig. 3.** Somatosensory evoked potential comparison. (A) Grand average SEP from Channels CP3 and CP4 to contralateral stimuli under attend and ignore conditions (left stimuli for CP4 and right stimuli for CP3). Three major SEP components, positivities at 50 and 100 ms and a negativity at 150 ms, are seen. Significant differences ( $P < 0.05$ , Wilcoxon signed-rank test) between the two conditions, marked by the horizontal yellow bars, are found in the range of the P1 (~50 ms) component and following the N1 (~150) component. (B) Grand average SEP to ipsilateral stimuli (left stimuli for CP3 and right stimuli for CP4). The activation is smaller for ipsilateral stimuli compared with contralateral stimuli, and no clear components are visible before 100 ms. A significant difference between conditions is seen in the range of the N150 component. (C) Grand average SEP computed using all stimuli (left and right for both CP3 and CP4). Significant differences are seen in the ranges of the P1 and N1 components. The difference between attend and ignore conditions in the 150 ms range is more prominent in this plot, due to the bilateral nature of the N1 component. (D) Topographic map of the voltage difference between the SEP to all attended stimuli and the SEP to all ignored stimuli in the time period from 140 to 160 ms. While an attention effect (greater negativity) can be seen in both left and right parietal areas, the effect is more pronounced in the right hemisphere. A greater frontal positivity in this time period for attended stimuli can also be seen. For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.

power analyses”, with the additional step of using the temporal mean of each condition (as opposed to the power at each time point) as the normalization value. As an example, the normalized mu power time course for the *ignore* condition in a single subject would be calculated as:  $\text{Normalized\_ignore}(t) = \text{ignore}(t) / (\text{temporal\_mean}(\text{ignore}) + \text{temporal\_mean}(\text{attend}) + \text{temporal\_mean}(\text{baseline})) / 3$ . A Wilcoxon signed-rank test was used to test whether the difference between two conditions was statistically significant at each time point.

## RESULTS

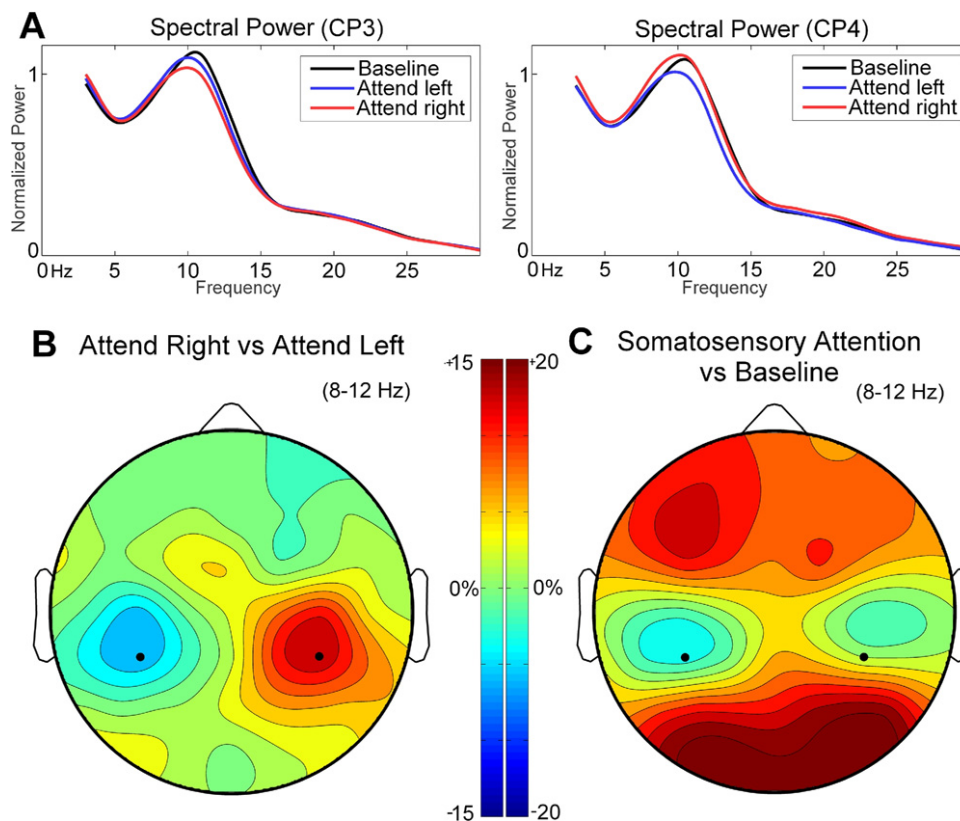
### Behavior

All 15 subjects performed the task according to instructions. The error-rate in target detection averaged across subjects for each condition was: 25.6% ( $\pm 2.3\%$ ) for attend-left and 25.5% ( $\pm 1.9\%$ ) for attend-right. This rate was maintained throughout the experiment by adjusting the amplitude of the target stimuli to ensure consistent task difficulty in both the attend-left and attend-right conditions.

The amplitudes of standard stimuli, which were held fixed at twice the detection threshold for each subject throughout the experiment, averaged across subjects were 2.71 mA ( $\pm 0.17$  mA) for right standard stimuli and 2.58 mA ( $\pm 0.14$  mA) for left standard stimuli. The generally higher detection threshold for the right hand, consistent with previous reports (Friedli et al., 1987; Meador et al., 1998), reflects handedness-related threshold asymmetry (all subjects in the current study were right-handed).

### Somatosensory evoked potential (SEP)

The grand average SEP waveforms for stimuli delivered contralaterally and ipsilaterally to recording electrodes over somatosensory cortex (CP3 and CP4) under attend and ignore conditions are shown in Fig. 3A, B. Data from the two hemispheres have been combined. The P1 component, sometimes also referred to as the P45, P50, or P60 component, peaks around 50 ms and is only seen in the hemisphere contralateral to stimulation. This component is significantly larger for the ignore condition compared with the attend condition. The N1 component, a bilateral negative component peaking around 150 ms and sometimes referred to as the N140, shows the opposite effect; a greater amplitude for attended stimuli than ignored stimuli. For contralateral stimuli, this negativity extends from 150 ms to 200 ms, overlapping a central positive component that peaks around 200 ms. Fig. 3C shows the grand average SEP for all stimuli (right and left) under attend and ignore conditions which emphasizes the bilateral N1 attention effect. The N1 effect is slightly larger in the right hemisphere as opposed to the left, as seen in Fig. 3D, which is a topographic plot of the mean difference between all attended stimuli (right stimulus, attend right; left stimulus, attend left) and all ignored stimuli (right stimulus, attend left; left stimulus, attend right) in the time period from 140 to 160 ms. This effect is consistent with a right hemispheric dominance in the parietal lobes during



**Fig. 4.** Prestimulus power comparison in the sensor space. (A) Normalized power spectra for each condition estimated for CP3 (left) and CP4 (right). At each channel, the power spectra for each condition in each subject were normalized by dividing the power at all frequencies by the average mu (8–12 Hz) band power of all three conditions. These two electrodes are represented by black dots on the topographic plots (B) and (C). Spectral power estimates from 0 to 3 Hz are contaminated due to high-pass filtering combined with  $1/f$  spectral characteristics, and are not shown. (B) The percent difference in prestimulus power in the 8–12 Hz band between attend-right and attend-left was computed according to the formula:  $(\text{Attend Right} - \text{Attend Left}) / ((\text{Attend Right} + \text{Attend Left}) / 2)$ . (C) The prestimulus power in the 8–12 Hz band from both somatosensory attention conditions is compared with the baseline condition. The percent difference between conditions was computed for each scalp sensor using the formula:  $((\text{Attend Left} + \text{Attend Right}) / 2 - \text{Baseline}) / \text{Baseline}$ . The two bars in the center of the plot indicate the scaling for the two plots. These plots were generated using EEGLAB's "topoplot" function (Delorme and Makeig, 2004). For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.

spatial attention (Heilman and Abell, 1980; Heilman et al., 1985; Mesulam, 1999; Meador et al., 2002).

#### Prestimulus power in 8–12 Hz: scalp level

In the period prior to stimulus onset, oscillatory activity can be used as a measure to give insight into the state of the brain and how directed attention modulates this state to facilitate information processing. Fig. 4 shows the effects of somatosensory attention on oscillations in the mu band (8–12 Hz) recorded at the scalp level.

Normalized prestimulus power spectra for sensors CP3 and CP4, averaged over all subjects, are plotted in Fig. 4A. A peak in the mu band (8–12 Hz) exists in both sensors for all conditions. It can also be seen in both sensors that the average prestimulus mu power measured over somatosensory cortex contralateral to the direction of attention is lower than the power over cortex ipsilateral to the direction of attention. A one-sided Wilcoxon signed-rank test of the difference in average mu power between attend-ipsilateral and attend-contralat-

eral resulted in  $P=0.11$  and  $P=0.06$  for CP3 and CP4, respectively.

Fig. 4B shows the average percent difference in 8–12 Hz band power between the attend-right and attend-left conditions over the entire scalp. Consistent with Fig. 4A, it can be seen that when somatosensory attention is directed to the right side, mu power over the contralateral (left) somatosensory cortex is lower than the mu power in the ipsilateral (right) somatosensory cortex. The effect appears to be localized to sensors lying over somatosensory cortex. Similar patterns of alpha power reduction have been observed over visual cortex with visual spatial attention (Thut et al., 2006; Rajagovindan and Ding, in press).

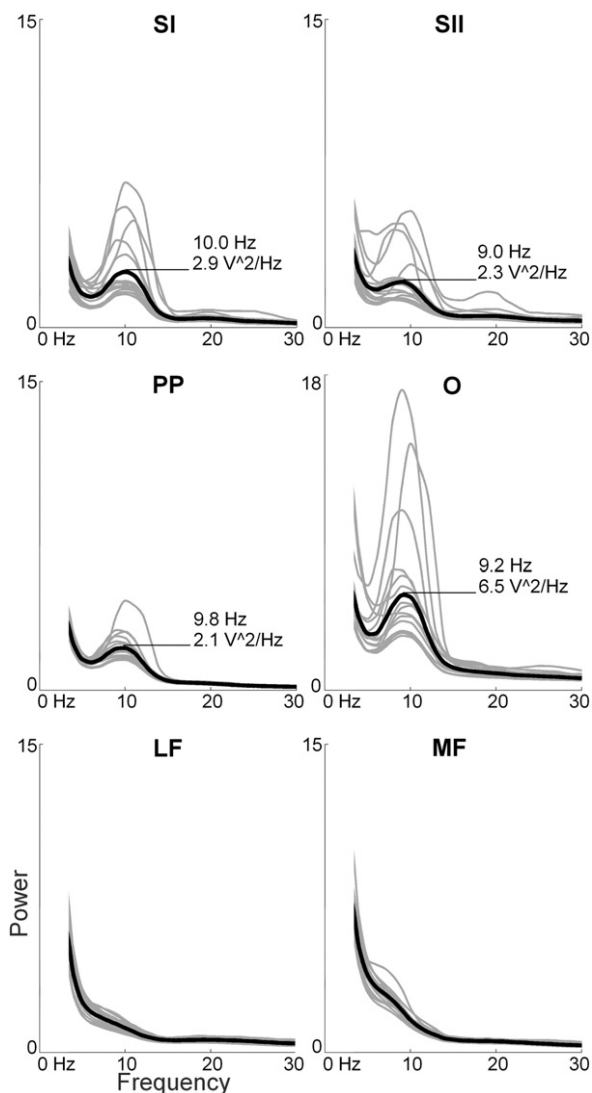
It is worth noting that while an attention-related decrease in mu power was seen in Fig. 4A, the difference was not highly significant ( $P=0.11$  for CP3 electrode and  $P=0.06$  for CP4 electrode). It is likely that, given the large visual alpha activity, the mu power estimation is adversely affected by volume conduction from the occipital cortex, which may also explain the broad increase in 8–12 Hz power during somatosensory attention compared with



baseline in brain areas outside the somatosensory cortex in Fig. 4C. This problem is overcome below by carrying out spectral power analysis in the source space.

### Prestimulus power in 8–12 Hz: source level

All power results in the following sections are obtained from the magnitude of the PSDs of the three components of each regional source dipole (see Experimental procedures). Fig. 5 shows the mean power spectra for the regional sources collapsed across conditions and hemispheres. Spectral power peaks in the 8–12 Hz range can



**Fig. 5.** Power spectral analysis in the source space. Gray curves represent power spectra from individual subjects and black curves are grand averages. Source abbreviations are: SI, primary somatosensory; SII, secondary somatosensory; PP, posterior parietal; O, occipital; LF, lateral frontal; MF, medial frontal. These power spectra were computed as the mean of the attend-left, attend-right, and baseline conditions, and have been combined across hemispheres (except for MF, which is a single, medial source). Peak amplitude and frequency in the mu band range (8–12 Hz) has been marked for the sources where a peak exists. Note that the Y-axis scale is different for the occipital source, while the scale is the same for all other sources.

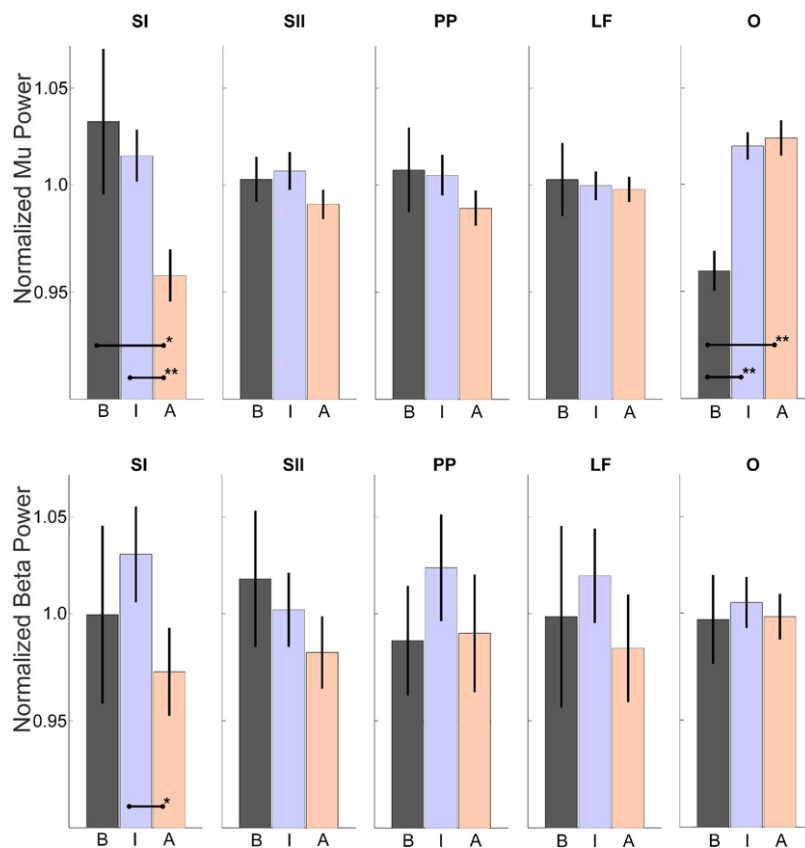
be seen in the somatosensory (SI, SII), posterior parietal (PP), and occipital (O) sources for all 15 subjects. A slight peak in the beta band (~20 Hz) can be seen in the SI and SII sources for two subjects and three subjects, respectively. The frontal sources, LF and MF, do not show peaks in the mu frequency range, though a slight bump in the theta range can be seen in some subjects. Spectral power estimates from 0 to 3 Hz are not plotted, as combining the high-pass action of the bandpass filtering with the 1/f spectral characteristic of the electroencephalography signal can create an artificial spectral peak in this frequency range (Slutzky, 1937; Demanuele et al., 2007).

The largest oscillations in the 8–12 Hz frequency band occur in the occipital sources, where the grand average peak is  $6.5 \text{ V}^2/\text{Hz}$ , compared with peaks of  $2.9 \text{ V}^2/\text{Hz}$ ,  $2.3 \text{ V}^2/\text{Hz}$ , and  $2.1 \text{ V}^2/\text{Hz}$  in SI, SII, and PP sources, respectively. If the somatosensory 8–12 Hz oscillations were due to voltage propagation from the occipital cortex, one would expect the amplitude of the oscillations measured from the posterior parietal sources (located between somatosensory and visual cortices) to lie between the amplitudes of the somatosensory and occipital oscillations. This is not the case, as the peak amplitude in the posterior parietal sources is less than the somatosensory sources as well as the occipital sources. Therefore somatosensory mu oscillations appear to be generated in local cortices. The 9.0 Hz peak seen in SII could represent the “sigma” rhythm, a 7–9 Hz rhythm recorded in SII that is responsive to somatosensory stimulation (Narici et al., 2001), though voltage propagation from SI cannot be ruled out.

One phenomenon to note is that mu activity was found in the SI sources of all 15 subjects. This finding contrasts with earlier reports where the incidence of observable mu oscillations in scalp EEG varied from 4% to 60% (Shaw, 2003). However, Niedermeyer (1997) hypothesized that the mu rhythm is a “universal phenomenon in healthy adolescents and adults” and McFarland et al. (2000) report that mu activity can be detected in most normal adults through spectral analysis of EEG activity.

Fig. 6 (top) shows the results of a comparison of mu band power between conditions in the source space. For a given source, the condition where attention is directed contralaterally to the source hemisphere is designated as the attend condition, and the condition where attention is directed ipsilaterally to the source hemisphere is designated as the ignore condition. The results are combined across hemispheres and band-power values for each subject were normalized according to the procedure described in “Spectral power analyses”.

For the primary somatosensory (SI) sources, a significant decrease in mu power is seen in the attend condition when compared with the ignore condition ( $P=0.002$ ) and baseline ( $P=0.031$ ). No significant difference is seen between the ignore and baseline conditions in SI ( $P=0.35$ ). In addition, 8–12 Hz (possibly sigma) oscillations in SII do not appear to be modulated by the current spatial attention task ( $P>0.1$  between all conditions), although past work has shown that attention modulates stimulus-evoked responses in SII (Hsiao et al., 1993; Mima et al., 1998;



**Fig. 6.** Mean mu 8–12 Hz band power (top) and beta 15–35 Hz band power (bottom) for all conditions normalized and averaged across subjects. Values for each regional source in both hemispheres have been combined. Source abbreviations are the same as in previous figures; condition abbreviations are: B, baseline; I, ignore; A, attend. Here “attend” or “ignore” refer to conditions where attention is directed either contralaterally or ipsilaterally to the source hemisphere. Error bars represent plus or minus one standard error of the mean. Lines between bars indicate a significant difference between conditions with one, and two stars signifying  $P$ -values less than 0.05, and 0.01, respectively, as measured by a Wilcoxon signed-rank test. For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.

Steinmetz et al., 2000; Fujiwara et al., 2002; Hoehstetter et al., 2002). No significant differences are found between conditions in the posterior parietal sources.

Power in the 8–12 Hz band is not significantly modulated in lateral frontal cortex by the current spatial attention task ( $P > 0.1$  between all conditions). The medial frontal source was not included in this analysis as it has no laterality, and thus “attend contralateral” and “attend ipsilateral” are undefined in the prestimulus period for this source.

In occipital cortex, a significant power increase is seen from baseline to somatosensory attention conditions ( $P = 0.000027$  for baseline vs. ignore and  $P = 0.000047$  for baseline vs. attend). This is consistent with the “gating” hypothesis that an increase in 10 Hz oscillations occurs over cortical areas that are irrelevant to the task (Foxe et al., 1998; Jensen et al., 2002; Cooper et al., 2003; Rihs et al., 2007; Klimesch et al., 2007).

#### Prestimulus power in 15–35 Hz: source level

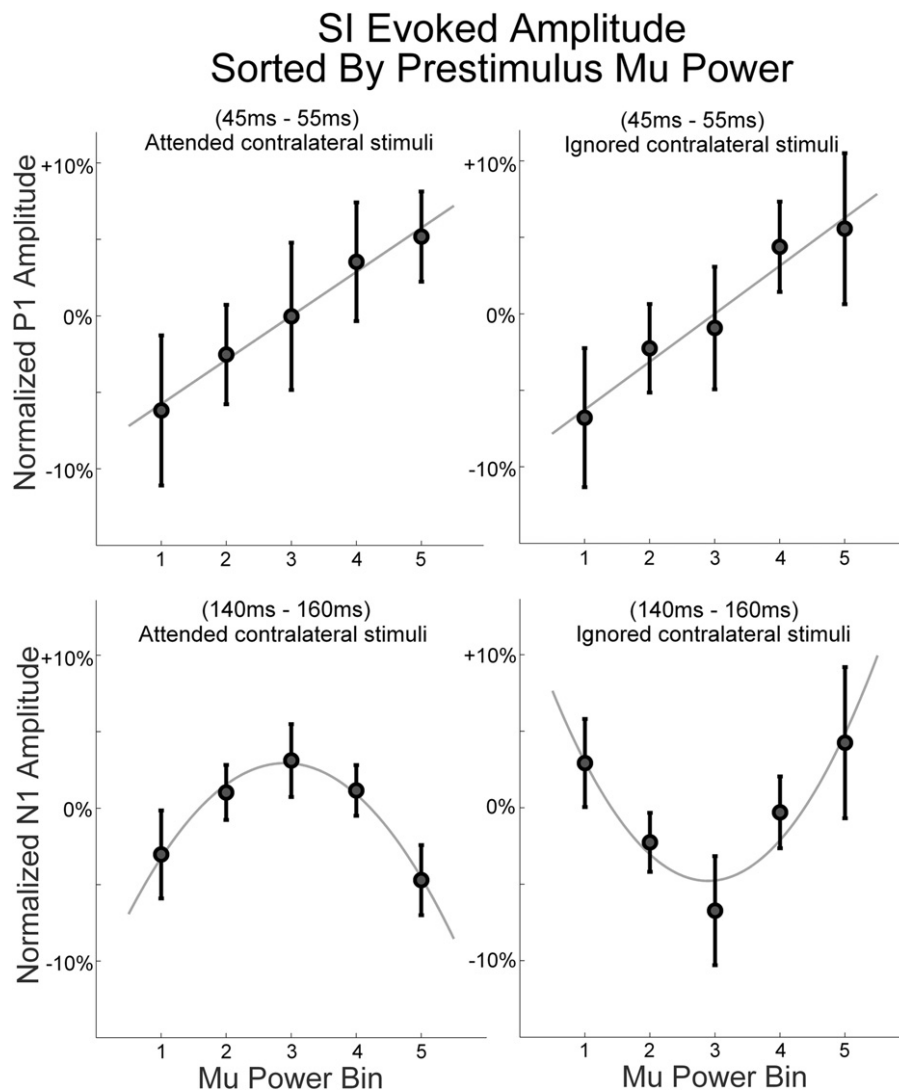
According to a previous MEG study (van Ede et al., 2010) beta band is defined to be 15–35 Hz. As shown in Fig. 6 (bottom) prestimulus beta power during the attend condition is significantly less than during the ignore condition

( $P = 0.048$ ) in the SI. Attention does not appear to significantly modulate beta oscillations in any of the other cortical areas. The larger error bars (standard errors of the mean) are likely due to the lack of precision in estimating beta power in the absence of consistent spectral peaks in this frequency range. Further analyses below will focus on the mu band, where the attention effects are more robust.

#### From prestimulus mu power to stimulus evoked activity

The above results showed that, over primary somatosensory cortex contralateral to the attended direction, attention reduced mu power prior to stimulus onset and at the same time modulated the stimulus-evoked response. Presumably, the prestimulus mu power reduction contributed to the subsequently improved stimulus processing. In order to investigate the relationship between pre- and post-stimulus activity, we estimated the magnitude of the evoked potential in SI for two time periods: 45 ms to 55 ms (early), and 140 ms to 160 ms (late) as a function of different levels of prestimulus mu power in the same hemisphere under the attend condition (attend contralaterally to source hemisphere) and the ignore condition (attend ipsilaterally to source hemisphere) (see Correlation between prestimulus mu power and evoked potential





**Fig. 7.** From prestimulus mu power to stimulus evoked response. For the SI source, the mean magnitude of evoked activity in two time periods: 45–55 ms (top left and right) and 140–160 ms (bottom left and right) is plotted as a function of prestimulus ongoing mu power. Evoked amplitudes have been normalized for each subject and averaged across subjects as described in “Correlation between prestimulus mu power and evoked potential amplitude”. Bin 1 represents the lowest prestimulus mu power while Bin 5 represents the highest prestimulus mu power. Error bars represent the standard error of the mean for each bin. Gray curves represent the fit regression curves, either linear or quadratic.

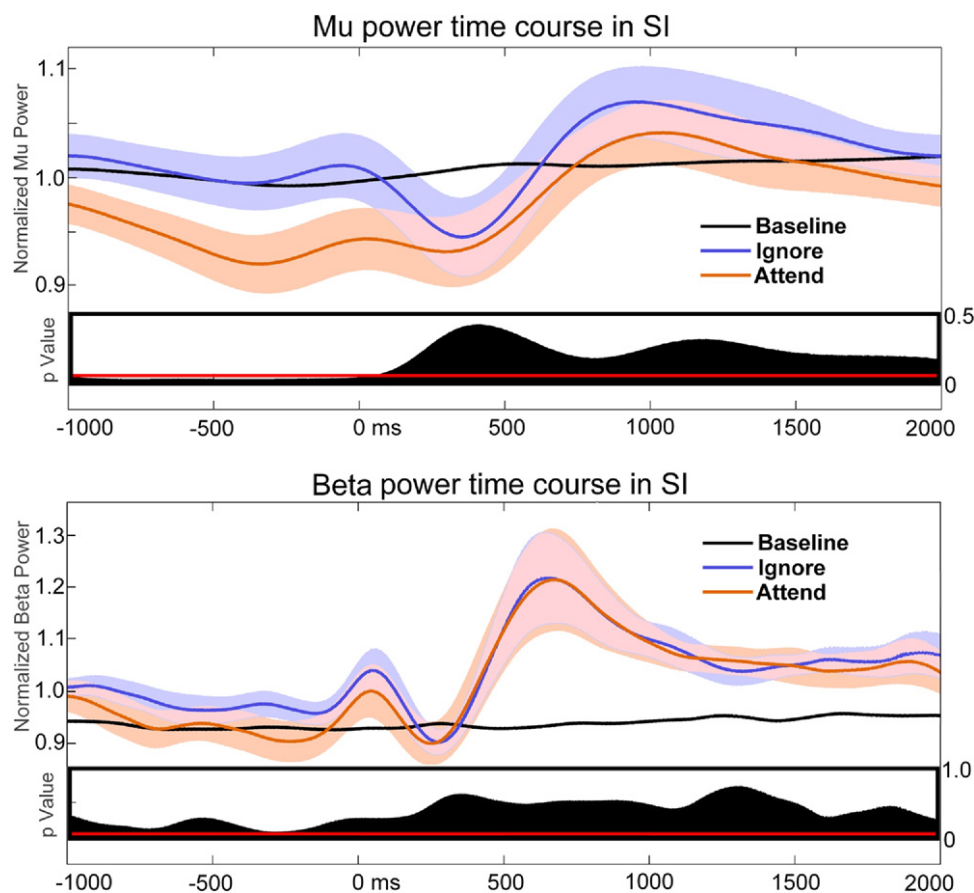
amplitude for details). Stimuli delivered contralateral to each SI source were included and results were combined across hemispheres. As seen in Fig. 7, a significant positive linear relationship was found between prestimulus mu power and the early evoked component for both attended and ignored stimuli (Spearman rank correlation  $\rho=0.26$ ,  $P=0.037$  for attended stimuli and  $\rho=0.29$ ,  $P=0.019$  for ignored stimuli). The later component followed a nonlinear quadratic relationship with prestimulus mu power in both conditions. For attended stimuli, the relationship was of an inverted U type, with a  $P$ -value for the F statistic of 0.041. The relationship for ignored stimuli followed an upright U shape with  $P=0.091$ .

The spatial specificity of the relationship between prestimulus mu power and evoked response was investigated by employing a similar analysis for the remaining sources. For each source, the time intervals chosen for analysis were

defined according to where a significant difference was found between the grand average evoked activity to attended and unattended contralateral somatosensory stimuli. These sources and the intervals are as follows: SII from 140 ms to 180 ms, PP from 85 ms to 110 ms and from 180 ms to 200 ms, and LF from 135 ms to 160 ms. No significant linear or quadratic relationships were seen between prestimulus 8–12 Hz power and evoked activity during these latencies to attended or unattended contralateral somatosensory stimuli in any of these regional sources.

#### Time-frequency analysis of mu and beta activity in SI

Fig. 8 (top) shows the mu power at the SI source as a function of time in the period from –1000 ms to 2000 ms where 0 ms denotes the onset of the standard stimulus or the artificially inserted trigger for the baseline condition. It



**Fig. 8.** Time course of mu (top) and beta (bottom) power in SI normalized and averaged across hemispheres and subjects. Shaded areas indicate one standard error of the mean. Here “attend” or “ignore” refer to conditions where attention is directed either contralaterally or ipsilaterally to the source hemisphere. The significance level of the difference between the ignore and attend conditions at each time point (as measured by a Wilcoxon signed-rank test) is plotted at the bottom of the figure. The red line indicates  $P=0.05$ . For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.

can be seen that the prestimulus mu power is significantly different between the attention conditions and this difference is diminished following stimulus input. This result demonstrates that the task-related effect seen in Fig. 6 is not due to bottom-up stimulus processing but top-down attention to the upcoming stimulus. A similar result is seen with beta power in Fig. 8 (bottom) but the effect is less significant.

## DISCUSSION

In this study, we investigated the effects of spatial somatosensory attention on stimulus processing and on prestimulus somatosensory mu (8–12 Hz) and visual alpha (8–12 Hz) band oscillations. For the two components of the somatosensory evoked potential investigated, the P1 was reduced with attention, while the N1 was enhanced with attention. At the sensor level, the power of the mu oscillations over somatosensory cortex contralateral to the attended direction and prior to stimulus onset was reduced by spatial attention in a manner similar to the reduction of alpha oscillations in visual cortex by visual spatial attention, though this effect did not reach significance. Interest-

ingly, the occipital alpha rhythm exhibited an intermodal attention effect, in that it was greatly elevated above baseline level during somatosensory attention. To more precisely localize attention effects, a spatial filtering method was used to estimate activity from multiple cortical sources, including bilateral SI, bilateral SII, bilateral posterior parietal, bilateral occipital, bilateral frontal, and medial frontal areas. A significant modulation of the mu rhythm according to direction of attention was observed in SI cortex, with a desynchronization occurring over SI contralateral to the direction of attention. A smaller, yet also significant, lateralized attention effect was also seen in the beta band (15 to 35 Hz). Additionally, a somatosensory attention related increase of visual alpha was seen in occipital sources. Lastly, a comparison of prestimulus mu power and evoked activity in SI revealed a positive linear relationship between mu and early (~50 ms) evoked activity for both attended and ignored stimuli, while a quadratic relationship was found between mu and later (~150 ms) evoked activity. This relationship between prestimulus mu and the later evoked component was dependent upon whether the stimulus was attended or ignored, having an

inverted U shape for attended stimuli and an upright U shape for ignored stimuli.

### Mu and attention

It has been postulated that field oscillations in the 10 Hz range should be characteristic of ongoing neuronal activity in every sensory cortex (Shaw, 2003). To date, the visual alpha rhythm has been the most extensively studied, and its active role in sensory processing as well as in higher order cognitive processes such as memory and attention has been firmly established (Klimesch et al., 2007; Palva and Palva, 2007; Rajagovindan and Ding, in press). One hallmark of visual alpha reactivity is its modulation by spatial attention, where an increase or decrease in the amplitude of alpha over visual cortex has been attributed to inhibition or facilitation, respectively, of visual stimulus processing (Klimesch et al., 2007; Romei et al., 2008).

Physiologically, alpha is considered to be a local reflection of the level of cortical excitability, with a smaller alpha amplitude being associated with greater excitability (Foxe et al., 1998; Jones et al., 2000, 2009; Worden et al., 2000; Bastiaansen and Brunia, 2001; Klimesch et al., 2007; Neuper et al., 2006). This hypothesis is supported by evidence from transcranial magnetic stimulation (TMS), which has found an inverse relationship between posterior alpha power and stimulation threshold for inducing illusory phosphenes (Romei et al., 2008). Further support for this hypothesis can be found in a recent study by Lee et al. (2010), which utilized optogenetics to determine a positive correlation between local neuronal excitation and blood oxygenation level-dependent (BOLD) signals detected with functional magnetic resonance imaging (fMRI). This finding, combined with negative correlations between local BOLD and alpha/mu band power from simultaneous recordings of EEG and fMRI (Goldman et al., 2002; Feige et al., 2005; Moosmann et al., 2003; de Munck et al., 2009; Ritter et al., 2009), is strong evidence for the inverse relationship between local 10 Hz power and cortical excitability.

Relative to visual alpha, the mu rhythm, measured over somatosensory cortex, is less well understood. Traditionally, the mu rhythm has been investigated in relation to its event related synchronization and desynchronization properties with respect to movement and stimulation. More recent work has begun to associate changes in the ongoing mu rhythm with higher-order cognitive processes such as working memory (Haegens et al., 2010) and anticipation (Babiloni et al., 2004, 2008). Jones et al. (2010), utilizing MEG, addressed the question of whether and how spatial attention modulates somatosensory mu and beta oscillations. They reported that spatial attention to the hand led to a decrease in mu power below baseline in the hand area of SI while spatial attention to the foot on the same side of the body was accompanied by a mu power increase above baseline in the same hand area. A similar, yet weaker effect was also seen in the beta band. Our study, utilizing EEG, confirms and extends this finding by showing that, prior to sensory input, sustained lateralized somatosensory spatial attention decreased the mu rhythm over so-

matosensory cortex contralateral to the direction of attention. We did not observe, however, a significant increase of mu power above baseline in somatosensory cortex ipsilateral to the direction of attention. This discrepancy could be explained by the difference in task requirements. In our task, attention is directed either to the left hand or right hand, while in the task of Jones et al. (2010), attention is directed to either the left hand or left foot. It is possible that directing somatosensory attention away from the hand, where somatosensory input is often consciously processed, to the foot, where conscious processing of input occurs less often, would require active inhibition of the hand area as well as facilitation of the foot area. It is thus conceivable that the mu activity in the foot area of SI would more closely match our results.

In the MEG modality, beta band activity is often analyzed along with mu activity in the 8–12 Hz band (Jones et al., 2010; van Ede et al., 2010). In EEG recordings, however, the beta rhythm is often not very prominent (Zhang and Ding, 2010). In the present work spectral peaks in the beta band were only observed in a small number of subjects. In the primary somatosensory cortex, a significant lateralized attention effect was found for prestimulus beta, with smaller beta over SI contralateral to the direction of attention compared with that over SI ipsilateral to the direction of attention. This result is similar to that of van Ede et al. (2010), who found a lateralized modulation of beta band activity in SI during expectation of a lateralized somatosensory stimulus. This effect was stronger during attentive expectation as compared with non-attentive expectation. No such effect was seen in the mu band.

In the visual domain, how alpha-band oscillations are modulated in visual areas representing ignored visual locations is also debated, with some groups reporting predominantly an increase in alpha power in these areas, while other groups report only a decrease in alpha power over cortex that represents attended locations. Still others have reported both effects simultaneously. This leads to a question of whether spatial attention is achieved through a suppression of irrelevant cortical processing, an enhancement of relevant cortical processing, or a combination of both. The answer appears to be that the relative contribution of enhancement and inhibition depends on the task. Three reports in the visual modality with findings similar to ours are: Sauseng et al. (2005), Thut et al. (2006), and Wyart and Tallon-Baudry (2008). All three used modified versions of the Posner cuing paradigm (Posner et al., 1978). These tasks, as with ours, involved only two directions of attention (left vs. right) and there were no simultaneously presented competing stimuli within a trial which would require active inhibition. In contrast to our findings, Worden et al. (2000) reported only an alpha increase ipsilateral to the direction of cued spatial attention, though this was not compared with a precue baseline. In fact, it appears that during the period immediately before the cue when attention has not yet been deployed, alpha power is higher bilaterally than during either attention condition. Contrary to the above mentioned reports, three papers which found, compared with a baseline period, primarily an

increase in alpha power ipsilateral to the direction of attention are: Yamagishi et al. (2003), Kelly et al. (2006), and Rihs et al. (2007). It appears that the discrepancy between their and our findings can be attributed to differences in the experimental tasks. Both Kelly et al. (2006) and Yamagishi et al. (2003) used tasks where stimuli to be attended and ignored were presented simultaneously within a trial, requiring active suppression of the ignored stimuli. Rihs et al. (2007) employed a more complicated cued spatial attention paradigm, where attention needed to be deployed to one of eight spatial locations around a fixation point. The authors suggested that the predominance of alpha increase could be due to the number of behaviorally relevant locations increasing the need for active inhibition.

It is worth noting that in our study, concurrent with the modulation of somatosensory mu, there is an intermodal effect in the visual domain where the occipital alpha rhythm is increased above baseline during somatosensory task conditions. This finding is consistent with the notion that an increase of alpha power reflects an active inhibition of visual processing (Klimesch et al., 2007). Such an increase in visual alpha power during attention to non-visual modalities has been reported previously (Foxe et al., 1998; Fu et al., 2001). Additionally, Pfurtscheller (1992) found an inverse relationship between somatomotor mu and visual alpha rhythms during both finger movement and reading tasks. During the reading task, a decrease in 10–12 Hz activity was seen over visual areas while an increase in 10–12 Hz activity (also known as event related synchronization or ERS) was seen over bilateral somatomotor areas. The reverse was found during the finger movement task. Further support for this idea comes from Haegens et al. (2010) who showed that occipital alpha power during the retention period in a somatosensory delayed-match-to-sample task is positively correlated with working memory performance as well as from Bollimunta et al. (2008) who found that higher levels of alpha activity recorded from early visual cortex in monkeys led to better reaction times to auditory stimuli.

We have interpreted the modulation of prestimulus mu power as being a result of the direction of spatial attention in anticipation of the upcoming stimulus (a top-down process). Due to the fact that the attention conditions were manipulated block-wise, as opposed to using a cued design, it is possible that this effect is due to an attentional modulation of the response to the previous stimulus (a bottom-up process). In order to investigate this, we compared the time courses of mu power in SI between conditions and found that while the prestimulus mu power is significantly different between the attention conditions, this difference is diminished following stimulus input. This result demonstrates that the task-related effect seen in Fig. 6 is not due to bottom-up stimulus processing but top-down attention to the upcoming stimulus.

### Evoked activity and attention

ERP analyses showed two effects due to spatial attention: a suppression of the P1 (~50 ms) component and an enhancement of the N1 (~150 ms) component with at-

tended stimuli. Nomenclature for these components in the literature varies with differing peak latencies due to task, stimulation site, and recording modality; we will refer to the initial positive peak occurring over contralateral somatosensory cortex around 50 ms after the stimulus as the P1 component and the large bilateral negative component peaking over posterior parietal cortex around 150 ms after the stimulus as the N1 component.

A greater stimulus evoked response in the N1 time window has been previously associated with attention (Michie, 1984; Garcia-Larrea et al., 1995; Forss et al., 1996; Eimer and Forster, 2003; Zopf et al., 2004) as well as stimulus detection and awareness (Libet et al., 1967; Schubert et al., 2006; Zhang and Ding, 2010). The topography of this effect varies between reports. In the current study, the N1 attention effect is most prominent over parietal electrodes and spatial filtering/source modeling indicates a contribution from SI (not shown). The N1 component measured in primary somatosensory cortex is thought to be generated in part due to excitatory feedback from higher-order areas to the superficial layers of SI (Cauller and Kulics, 1991; Cauller et al., 1998). This feedback could be a key process in the conscious perception of stimuli and a larger N1 could indicate a greater level of higher-order stimulus processing occurring for attended as opposed to ignored stimuli.

The evoked somatosensory P1 component has been found to vary in amplitude with stimulus intensity. However, previous research has also found it to be affected by endogenous factors (Tomberg and Desmedt, 1996; Schubert et al., 2008). In the current study, the intensity of standard stimuli was kept constant within each subject, so modulations of evoked activity can be attributed to cognitive processes such as attention. Our finding of an enhanced P1 component for ignored stimuli is consistent with Jones et al. (2010), who reported a positive SEF component (M50) peaking at 50 ms to be of a greater amplitude following ignored as opposed to attended vibrotactile stimuli. This result conflicts with the findings of Schubert et al. (2008), however, who reported an attentional enhancement of this component during a cued somatosensory spatial attention task. Others have reported no difference in P1 amplitude due to spatial attention (Eimer and Forster, 2003; Zopf et al., 2004). The conflicting results could be due to a difference in task design, as ours was a sustained as opposed to a cued attention task. In fact, Eimer and Forster's (2003) results obtained from a sustained spatial attention task show a trend toward a suppression of P1 with attention, though it was not reported as being statistically significant. In the current experiment, the significant effect of sustained attention on the evoked P1 component, which is considered to be generated in SI by purely feed-forward mechanisms, supports the theory of sensory gain control occurring at early stages of cortical processing (Hillyard et al., 1998).

A suppression of early evoked activity by attention may seem counterintuitive. One possible explanation is that some aspect of the P1 component could represent local inhibition. With a mean latency of around 50 ms, the P1 is



not the earliest cortical evoked response; the N20/P20 complex is the first cortically generated activity recorded on the scalp in humans, and is generated by the initial excitatory input to area 3b from the thalamus (Wood et al., 1985; Lee and Seyal, 1998). The P20 in monkeys, which is analogous to the human somatosensory P1 (Allison et al., 1992; Arezzo et al., 1981), is associated with increased neural activity in middle cortical layers (Kulics and Cauller, 1986), and simultaneous excitatory and inhibitory activity (Peterson et al., 1995). Wikström et al. (1996) hypothesized that SI activity in humans between 45 and 60 ms could correspond with local inhibitory post synaptic potentials (IPSPs) occurring after the initial thalamocortical volley. This is supported by the neural model of Jones et al. (2009), which predicts a larger 50 ms evoked response in SI to be associated with an increased activation of excitatory neurons which subsequently activate inhibitory neurons, resulting in a suppression of subsequent “feedback” evoked components. The inverse relationship between early activity (P1) generated in middle layers and later activity (N1) generated in superficial layers could possibly be related to acetylcholine release during sustained attention (Himmelheber et al., 2000), which has been found to have a hyperpolarizing effect on layer IV stellate cells while depolarizing pyramidal neurons in layers II/III and layer V in rat SI cortex (Eggermann and Feldmeyer, 2009).

#### Relationship between prestimulus mu and evoked activity

It is reasonable to speculate that the prestimulus mu desynchronization due to attention contributed to the subsequently improved stimulus processing by attention. The relationship between prestimulus mu oscillations and stimulus processing has been investigated previously. Linkenkaer-Hansen et al. (2004) and Zhang and Ding (2010) both found that the amplitude of prestimulus mu oscillations predicts subsequent perception of a threshold-level somatosensory stimulus, with an intermediate level of mu leading to better stimulus detection. Further evidence of the relationship between ongoing mu activity and subsequent stimulus processing can be seen in the results of Nikouline et al. (2000b), Reinacher et al. (2009), Zhang and Ding (2010), and Jones et al. (2009, 2010), who all reported correlations between prestimulus mu power and the amplitude of stimulus evoked activity. Zhang and Ding (2010), using EEG, found an inverted-U relationship between mu power and the somatosensory evoked N1 component. A similar finding has also been made in the visual domain between alpha power and the visual evoked P1 component (Rajagovindan and Ding, in press). In contrast, Reinacher et al. (2009) reported a larger negative frontal-midline component occurring 140 ms after suprathreshold stimuli delivered during periods of high mu activity, as compared with the same stimuli delivered without mu triggering. Both Nikouline et al. (2000b) and Jones et al. (2009) found a positive linear relationship between mu and early evoked components occurring around 50–60 ms measured with MEG. The positive correlation found by Jones et al. (2009) was predicted by a neural model de-

veloped in the same study. This model predicted an inverse relationship between mu and later evoked activity occurring 135 ms post-stimulus, though this result was not found in their experimental data.

In the current experiment, we found a positive linear relationship between prestimulus mu power and the magnitude of early evoked activity (~50 ms) in SI, in agreement with the findings of Nikouline et al. (2000b) and Jones et al. (2009) mentioned above. Interestingly, the relationship between early evoked activity and prestimulus mu was the same for both attended and ignored stimuli. This might be an indication of a direct physiological correlation between the level of mu activity and the generation of the somatosensory P1 component.

For the later evoked activity (~150 ms) after attended stimuli, its magnitude follows an inverted U function in relation to prestimulus mu power. This is consistent with the findings of Zhang and Ding (2010) and suggests that, in the attentive state, the most effective information processing occurs with an intermediate level of mu activity in the somatosensory cortex (Linkenkaer-Hansen et al., 2004; Zhang and Ding, 2010). A theory has been proposed by Rajagovindan and Ding (in press) to explain a similar relationship between occipital alpha oscillations and visually evoked P1 responses. However, for ignored stimuli during the current task, both high and low amplitudes of prestimulus mu corresponded to a larger evoked response, leading to an upright U relationship between prestimulus mu and later evoked activity. To our knowledge, this effect has not been reported and does not appear to fit well with existing models. It is possible that the smaller amplitude of the N1 component evoked by ignored stimuli, compared to attended stimuli, affected its proper estimation, as the *P*-value of the quadratic fit for this condition was not quite significant ( $P=0.091$ ). The fact that no significant linear or quadratic relationships between prestimulus 8–12 Hz power and evoked response to contralateral somatosensory stimuli were found in the remaining regional sources suggests that these pre- and post-stimulus relationships are specific to primary somatosensory cortex.

#### CONCLUSION

Our analyses support the view that ~10 Hz oscillations are a ubiquitous phenomenon in sensory cortex, and that these oscillations are involved in higher cognitive functions such as attention. Specifically, we found that during sustained lateralized somatosensory spatial attention, the mu rhythm is somatotopically modulated in a way similar to the visual alpha rhythm during spatial attention in the visual domain. The increase in visual alpha activity during attention to the somatosensory domain suggests that these rhythms are involved with suppressing irrelevant input in addition to facilitating relevant input. Finally, our finding that early (P1) and later (N1) evoked activity are both influenced by, yet follow different relationships with, the level of prestimulus mu power indicates that these oscillations might be working at multiple levels to impact sensory processing.

## REFERENCES

- Allison T, McCarthy G, Wood CC (1992) The relationship between human long-latency somatosensory evoked potentials recorded from the cortical surface and from the scalp. *Electroencephalogr Clin Neurophysiol* 84(4):301–314.
- Arezzo JC, Vaughan HG, Legatt AD (1981) Topography and intracranial sources of somatosensory evoked potentials in the monkey. II. Cortical components. *Electroencephalogr Clin Neurophysiol* 51(1):1–18.
- Babiloni C, Brancucci A, Arendt-Nielsen L, Babiloni F, Capotosto P, Carducci F, Cincotti F, Del Percio C, Petrini L, Rossini PM, Chen AC (2004) Attentional processes and cognitive performance during expectancy of painful galvanic stimulations: a high-resolution EEG study. *Behav Brain Res* 152(1):137–147.
- Babiloni C, Capotosto P, Brancucci A, Del Percio C, Petrini L, Buttiglionone M, Cibelli G, Luca Romani G, Maria Rossini P, Arendt-Nielsen L (2008) Cortical alpha rhythms are related to the anticipation of sensorimotor interaction between painful stimuli and movements: a high resolution EEG study. *J Pain* 9(10):902–911.
- Bastiaansen MCM, Brunia CHM (2001) Anticipatory attention: an event-related desynchronization approach. *Int J Psychophysiol* 43(1):91–107.
- Bollimunta A, Chen Y, Schroeder CE, Ding M (2008) Neuronal mechanisms of cortical alpha oscillations in awake-behaving macaques. *J Neurosci* 28(40):9976–9988.
- Bowsher D, Brooks J, Enevoldson P (2004) Central representation of somatic sensations in the parietal operculum (SII) and insula. *Eur Neurol* 52(4):211–225.
- Caulier LJ, Kulics AT (1991) The neural basis of the behaviorally relevant N1 component of the somatosensory-evoked potential in SI cortex of awake monkeys: evidence that backward cortical projections signal conscious touch sensation. *Exp Brain Res* 84(3):607–619.
- Caulier LJ, Clancy B, Connors BW (1998) Backward cortical projections to primary somatosensory cortex in rats extend long horizontal axons in layer I. *J Comp Neurol* 390(2):297–310.
- Cooper NR, Croft RJ, Dominey SJJ, Burgess AP, Gruzeliier JH (2003) Paradox lost? Exploring the role of alpha oscillations during externally vs. internally directed attention and the implications for idling and inhibition hypotheses. *Int J Psychophysiol* 47(1):65–74.
- Corbetta M, Akbudak E, Conturo T, Snyder A, Ollinger J, Drury H, Linenweber M, Petersen SE, Raichle ME, Van Essen DC, Shulman GL (1998) A common network of functional areas for attention and eye movements. *Neuron* 21(4):761–773.
- de Munck JC, Gonçalves SI, Mammoliti R, Heethaar RM, Lopes da Silva FH (2009) Interactions between different EEG frequency bands and their effect on alpha-fMRI correlations. *Neuroimage* 47(1):69–76.
- Della Penna S, Torquati K, Pizzella V, Babiloni C, Franciotti R, Rossini PM, Romani GL (2004) Temporal dynamics of alpha and beta rhythms in human SI and SII after galvanic median nerve stimulation. A MEG study. *Neuroimage* 22(4):1438–1446.
- 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(1):9–21.
- Demanuele C, James CJ, Sonuga-Barke EJ (2007) Distinguishing low frequency oscillations within the 1/f spectral behaviour of electromagnetic brain signals. *Behav Brain Funct* 3:62.
- Dougherty RF, Koch VM, Brewer AA, Fischer B, Modersitzki J, Wandell BA (2003) Visual field representations and locations of visual areas V1/2/3 in human visual cortex. *J Vis* 3(10):586–598.
- Eggermann E, Feldmeyer D (2009) Cholinergic filtering in the recurrent excitatory microcircuit of cortical layer 4. *Proc Natl Acad Sci U S A* 106(28):11753–11758.
- Eickhoff SB, Amunts K, Mohlberg H, Zilles K (2006) The human parietal operculum. II. Stereotaxic maps and correlation with functional imaging results. *Cereb Cortex* 16(2):268–279.
- Eimer M, Forster B (2003) Modulations of early somatosensory ERP components by transient and sustained spatial attention. *Exp Brain Res* 151(1):24–31.
- Feige B, Scheffler K, Esposito F, Di Salle F, Hennig J, Seifritz E (2005) Cortical and subcortical correlates of electroencephalographic alpha rhythm modulation. *J Neurophysiol* 93(5):2864–2872.
- Forss N, Merlet I, Vanni S, Hamalainen M, Manguiere F, Hari R (1996) Activation of human mesial cortex during somatosensory target detection task. *Brain Res* 734(1–2):229–235.
- Foxe JJ, Simpson GV, Ahlfors SP (1998) Parieto-occipital approximately 10 Hz activity reflects anticipatory state of visual attention mechanisms. *Neuroreport* 9(17):3929–3933.
- Friedli WG, Fuhr P, Wiget W (1987) Detection threshold for percutaneous electrical stimuli: asymmetry with respect to handedness. *J Neurol Neurosurg Psychiatry* 50(7):870–876.
- Fu KG, Foxe JJ, Murray MM, Higgins BA, Javitt DC, Schroeder CE (2001) Attention-dependent suppression of distracter visual input can be cross-modally cued as indexed by anticipatory parieto-occipital alpha-band oscillations. *Brain Res Cogn Brain Res* 12(1):145–152.
- Fujiwara N, Imai M, Nagamine T, Mima T, Oga T, Takeshita K, Toma K, Shibasaki H (2002) Second somatosensory area (SII) plays a significant role in selective somatosensory attention. *Brain Res Cogn Brain Res* 14(3):389–397.
- Gaetz W, Cheyne D (2006) Localization of sensorimotor cortical rhythms induced by tactile stimulation using spatially filtered MEG. *Neuroimage* 30(3):899–908.
- Garcia-Larrea L, Lukasiewicz A, Maguier F (1995) Somatosensory responses during selective spatial attention: the N120-to-N140 transition. *Psychophysiology* 32(6):526–537.
- Gastaut H (1952) Electroencephalographic study of the reactivity of Rolandic rhythm. *Rev Neurol (Paris)* 87(2):176–182.
- Goldman RI, Stern JM, Engel J, Cohen MS (2002) Simultaneous EEG and fMRI of the alpha rhythm. *Neuroreport* 13(18):2487–2492.
- Haegens S, Osipova D, Oostenveld R, Jensen O (2010) Somatosensory working memory performance in humans depends on both engagement and disengagement of regions in a distributed network. *Hum Brain Mapp* 31(1):26–35.
- Heilman KM, Watson RT, Valenstein E (1985) Neglect and related disorders. In: *Clinical neuropsychology*, 2nd ed (Heilman KM, Valenstein E, eds), pp 268–307. New York: Oxford University Press.
- Heilman KM, Abell TVD (1980) Right hemisphere dominance for attention: the mechanism underlying hemispheric asymmetries of inattention (neglect). *Neurology* 30(3):327.
- Hillyard SA, Vogel EK, Luck SJ (1998) Sensory gain control (amplification) as a mechanism of selective attention: electrophysiological and neuroimaging evidence. *Philos Trans R Soc Lond B Biol Sci* 353(1373):1257–1270.
- Himmelheber AM, Sarter M, Bruno JP (2000) Increases in cortical acetylcholine release during sustained attention performance in rats. *Brain Res Cogn Brain Res* 9(3):313–325.
- Hoechstetter K, Rupp A, Meinck HM, Weckesser D, Bornfleth H, Stippich C, Berg P, Scherg M (2002) Magnetic source imaging of tactile input shows task-independent attention effects in SII. *Neuroreport* 11(11):2461–2465.
- Hsiao SS, O'Shaughnessy DM, Johnson KO (1993) Effects of selective attention on spatial form processing in monkey primary and secondary somatosensory cortex. *J Neurophysiol* 70(1):444–447.
- Jensen O, Gelfand J, Kounios J, Lisman JE (2002) Oscillations in the alpha band (9–12 Hz) increase with memory load during retention in a short-term memory task. *Cereb Cortex* 12(8):877–882.
- Jokisch D, Jensen O (2007) Modulation of gamma and alpha activity during a working memory task engaging the dorsal or ventral stream. *J Neurosci* 27(12):3244–3251.
- Jones SR, Pinto DJ, Kaper TJ, Kopell N (2000) Alpha-frequency rhythms desynchronize over long cortical distances: a modeling study. *J Comput Neurosci* 9(3):271–291.

- Jones SR, Pritchett DL, Sikora MA, Stufflebeam SM, Hamalainen M, Moore CI (2009) Quantitative analysis and biophysically realistic neural modeling of the MEG mu rhythm: rhythmogenesis and modulation of sensory-evoked responses. *J Neurophysiol* 102(6):3554–3572.
- Jones SR, Kerr CE, Wan Q, Pritchett DL, Hämäläinen M, Moore CI (2010) Cued spatial attention drives functionally relevant modulation of the mu rhythm in primary somatosensory cortex. *J Neurosci* 30(41):13760–13765.
- Kastner S, Ungerleider LG (2000) Mechanisms of visual attention in the human cortex. *Annu Rev Neurosci* 23(1):315–341.
- Kelly SP, Lalor EC, Reilly RB, Foxe JJ (2006) Increases in alpha oscillatory power reflect an active retinotopic mechanism for distracter suppression during sustained visuospatial attention. *J Neurophysiol* 95(6):3844–3851.
- Klimesch W, Doppelmayr M, Schwaiger J, Auinger P, Winkler T (1999) Paradoxical alpha synchronization in a memory task. *Brain Res Cogn Brain Res* 7(4):493–501.
- Klimesch W, Sauseng P, Hanslmayr S (2007) EEG alpha oscillations: the inhibition-timing hypothesis. *Brain Res Rev* 53(1):63–88.
- Kulics AT, Cauller LJ (1986) Cerebral cortical somatosensory evoked responses, multiple unit activity and current source-densities: their interrelationships and significance to somatic sensation as revealed by stimulation of the awake monkey's hand. *Exp Brain Res* 62(1):46–60.
- Lee EK, Seyal M (1998) Generators of short latency human somatosensory-evoked potentials recorded over the spine and scalp. *J Clin Neurophysiol* 15(3):227–234.
- Lee JH, Durand R, Gradinaru V, Zhang F, Goshen I, Kim D, Fenno LE, Ramakrishnan C, Deisseroth K (2010) Global and local fMRI signals driven by neurons defined optogenetically by type and wiring. *Nature* 465:788–792.
- Leek MR (2001) Adaptive procedures in psychophysical research. *Percept Psychophys* 63(8):1279–1292.
- Libet B, Alberts WW, Wright EW, Feinstein B (1967) Responses of human somatosensory cortex to stimuli below threshold for conscious sensation. *Science* 158(3508):1597–1600.
- Linkenkaer-Hansen K, Nikulin VV, Palva S, Ilmoniemi RJ, Palva JM (2004) Prestimulus oscillations enhance psychophysical performance in humans. *J Neurosci* 24(45):10186–10190.
- McFarland D, Miner L, Vaughan T, Wolpaw J (2000) Mu and beta rhythm topographies during motor imagery and actual movements. *Brain Topogr* 12(3):177–186.
- Meador KJ, Ray PG, Day L, Ghelani H, Loring DW (1998) Physiology of somatosensory perception: cerebral lateralization and extinction. *Neurology* 51(3):721–727.
- Meador KJ, Allison J, Loring D, Lavin T, Pillai J (2002) Topography of somatosensory processing: cerebral lateralization and focused attention. *J Int Neuropsychol Soc* 8(3):349–359.
- Medendorp WP, Kramer GF, Jensen O, Oostenveld R, Schoffelen J, Fries P (2007) Oscillatory activity in human parietal and occipital cortex shows hemispheric lateralization and memory effects in a delayed double-step saccade task. *Cereb Cortex* 17(10):2364–2374.
- Mesulam M (1999) Spatial attention and neglect: parietal, frontal and cingulate contributions to the mental representation and attentional targeting of salient extrapersonal events. *Philos Trans R Soc Lond B Biol Sci* 354(1387):1325–1346.
- Michie PT (1984) Selective attention effects on somatosensory event-related potentials. *Ann N Y Acad Sci* 425:250–255.
- Mima T, Nagamine T, Nakamura K, Shibasaki H (1998) Attention modulates both primary and second somatosensory cortical activities in humans: a magnetoencephalographic study. *J Neurophysiol* 80(4):2215–2221.
- Moosmann M, Ritter P, Krastel I, Brink A, Thees S, Blankenburg F, Taskin B, Obrig H, Villringer A (2003) Correlates of alpha rhythm in functional magnetic resonance imaging and near infrared spectroscopy. *Neuroimage* 20(1):145–158.
- Narici L, Forss N, Jousmäki V, Peresson M, Hari R (2001) Evidence for a 7- to 9-Hz “sigma” rhythm in the human SII cortex. *Neuroimage* 13(4):662–668.
- Neuper C, Wörtz M, Pfurtscheller G (2006) ERD/ERS patterns reflecting sensorimotor activation and deactivation. *Prog Brain Res* 159:211–222.
- Niedermeyer E (1997) Alpha rhythms as physiological and abnormal phenomena. *Int J Psychophysiol* 26(1–3):31–49.
- Nikouline VV, Linkenkaer-Hansen K, Wikström H, Kesäniemi M, Antonova EV, Ilmoniemi RJ, Huttunen J (2000a) Dynamics of mu-rhythm suppression caused by median nerve stimulation: a magnetoencephalographic study in human subjects. *Neurosci Lett* 294(3):163–166.
- Nikouline VV, Wikström H, Linkenkaer-Hansen K, Kesäniemi M, Ilmoniemi RJ, Huttunen J (2000b) Somatosensory evoked magnetic fields: relation to pre-stimulus mu rhythm. *Clin Neurophysiol* 111(7):1227–1233.
- Palva S, Palva JM (2007) New vistas for alpha-frequency band oscillations. *Trends Neurosci* 30(4):150–158.
- Peterson NN, Schroeder CE, Arezzo JC (1995) Neural generators of early cortical somatosensory evoked potentials in the awake monkey. *Electroencephalogr Clin Neurophysiol* 96(3):248–260.
- Pfurtscheller G (1989) Functional topography during sensorimotor activation studied with event-related desynchronization mapping. *J Clin Neurophysiol* 6(1):75–84.
- Pfurtscheller G, Aranibar A, Maresch H (1979) Amplitude of evoked potentials and degree of event-related desynchronization (ERD) during photic stimulation. *Electroencephalogr Clin Neurophysiol* 47(1):21–30.
- Pfurtscheller G (1992) Event-related synchronization (ERS): an electrophysiological correlate of cortical areas at rest. *Electroencephalogr Clin Neurophysiol* 83:62–69.
- Pfurtscheller G, Neuper C, Mohl W (1994) Event-related desynchronization (ERD) during visual processing. *Int J Psychophysiol* 16(2–3):147–153.
- Pfurtscheller G, Lopes da Silva FH (1999) Event-related EEG/MEG synchronization and desynchronization: basic principles. *Clin Neurophysiol* 110:1842–1857.
- Posner MI, Nissen MJ, Ogden WC (1978) Attended and unattended processing modes: the role of set for spatial location. In: *Modes of perception* (Pick HJ, Saltzman IJ, eds), pp 137–157. Hillsdale, NJ: Erlbaum.
- Rajagovindan R, Ding M (in press) From prestimulus alpha oscillation to visual-evoked response: an inverted-U function and its attentional modulation. *J Cogn Neurosci*, in press.
- Reinacher M, Becker R, Villringer A, Ritter P (2009) Oscillatory brain states interact with late cognitive components of the somatosensory evoked potential. *J Neurosci Methods* 183(1):49–56.
- Rihs TA, Michel CM, Thut G (2007) Mechanisms of selective inhibition in visual spatial attention are indexed by alpha-band EEG synchronization. *Eur J Neurosci* 25(2):603–610.
- Ritter P, Moosmann M, Villringer A (2009) Rolandic alpha and beta EEG rhythms' strengths are inversely related to fMRI-BOLD signal in primary somatosensory and motor cortex. *Hum Brain Mapp* 30(4):1168–1187.
- Romei V, Rihs T, Brodbeck V, Thut G (2008) Resting electroencephalogram alpha-power over posterior sites indexes baseline visual cortex excitability. *Neuroreport* 19(2):203–208.
- Salenius S, Schnitzler A, Salmelin R, Jousmäki V, Hari R (1997) Modulation of human cortical rolandic rhythms during natural sensorimotor tasks. *Neuroimage* 5:221–228.
- Sauseng P, Klimesch W, Stadler W, Schabus M, Doppelmayr M, Hanslmayr S, Gruber WR, Birbaumer N (2005) A shift of visual spatial attention is selectively associated with human EEG alpha activity. *Eur J Neurosci* 22(11):2917–2926.
- Scherg M (1992) Functional imaging and localization of electromagnetic brain activity. *Brain Topogr* 5(2):103–111.

- Schira MM, Tyler CW, Breakspear M, Spehar B (2009) The foveal confluence in human visual cortex. *J Neurosci* 29(28):9050–9058.
- Schubert R, Blankenburg F, Lemm S, Villringer A, Curio G (2006) Now you feel it, now you don't: ERP correlates of somatosensory awareness. *Psychophysiology* 43(1):31–40.
- Schubert R, Ritter P, Wustenberg T, Preuschhof C, Curio G, Sommer W, Villringer A (2008) Spatial attention related SEP amplitude modulations covary with BOLD signal in S1—a simultaneous EEG—fMRI study. *Cereb Cortex* 18(11):2686–2700.
- Shaw JC (2003) The brain's alpha rhythms and the mind: a review of classical and modern studies of the alpha rhythm component of the electroencephalogram with commentaries on associated neuroscience and neuropsychology. Amsterdam, The Netherlands: Elsevier Science Ltd.
- Slutzky E (1937) The summation of random causes as the source of cyclic processes. *Econometrica* 5(2):105–146.
- Steinmetz PN, Roy A, Fitzgerald PJ, Hsiao SS, Johnson KO, Niebur E (2000) Attention modulates synchronized neuronal firing in primate somatosensory cortex. *Nature* 404(6774):180–190.
- Thut G, Nietzel A, Brandt SA, Pascual-Leone A (2006) Alpha-band electroencephalographic activity over occipital cortex indexes visuospatial attention bias and predicts visual target detection. *J Neurosci* 26(37):9494–9502.
- Tomberg C, Desmedt JE (1996) Non-averaged human brain potentials in somatic attention: the short-latency cognition-related P40 component. *J Physiol* 496 (Pt 2):559–574.
- Tuladhar AM, Huurne NT, Schoffelen J, Maris E, Oostenveld R, Jensen O (2007) Parieto-occipital sources account for the increase in alpha activity with working memory load. *Hum Brain Mapp* 28(8):785–792.
- Valeriani M, Restuccia D, Di Lazzaro V, Le Pera D, Tonali P (1997) The pathophysiology of giant SEPs in cortical myoclonus: a scalp topography and dipolar source modelling study. *Electroencephalogr Clin Neurophysiol* 104(2):122–131.
- van Ede F, Jensen O, Maris E (2010) Tactile expectation modulates pre-stimulus beta-band oscillations in human sensorimotor cortex. *Neuroimage* 51(2):867–876.
- Vijn PC, van Dijk BW, Spekreijse H (1991) Visual stimulation reduces EEG activity in man. *Brain Res* 550(1):49–53.
- Waberski TD, Gobbele R, Darvas F, Schmitz S, Buchner H (2002) Spatiotemporal imaging of electrical activity related to attention to somatosensory stimulation. *Neuroimage* 17(3):1347–1357.
- Wikström H, Huttunen J, Korvenoja A, Virtanen J, Salonen O, Aronen H, Ilmoniemi RJ (1996) Effects of interstimulus interval on somatosensory evoked magnetic fields (SEFs): a hypothesis concerning SEF generation at the primary sensorimotor cortex. *Electroencephalogr Clin Neurophysiol* 100(6):479–487.
- Wood C, Cohen D, Cuffin B, Yarita M, Allison T (1985) Electrical sources in human somatosensory cortex: identification by combined magnetic and potential recordings. *Science* 227(4690):1051–1053.
- Worden MS, Foxe JJ, Wang N, Simpson GV (2000) Anticipatory biasing of visuospatial attention indexed by retinotopically specific alpha-band electroencephalography increases over occipital cortex. *J Neurosci* 20(6):RC63.
- Wyart V, Tallon-Baudry C (2008) Neural dissociation between visual awareness and spatial attention. *J Neurosci* 28(10):2667–2679.
- Yamagishi N, Callan DE, Goda N, Anderson SJ, Yoshida Y, Kawato M (2003) Attentional modulation of oscillatory activity in human visual cortex. *Neuroimage* 20(1):98–113.
- 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(2):307–322.
- Zopf R, Giabbiconi CM, Gruber T, Müller MM (2004) Attentional modulation of the human somatosensory evoked potential in a trial-by-trial spatial cueing and sustained spatial attention task measured with high density 128 channels EEG. *Brain Res Cogn Brain Res* 20(3):491–509.

(Accepted 1 February 2011)  
(Available online 22 February 2011)