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## Cued Spatial Attention Drives Functionally-Relevant Modulation of The Mu Rhythm in Primary Somatosensory Cortex

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### Abstract

Cued spatial attention modulates functionally relevant alpha rhythms in visual cortices in humans. Here, we present evidence for analogous phenomena in primary somatosensory neocortex (SI). Using magnetoencephalography (MEG), we measured changes in the SI mu rhythm containing mu-alpha (7-14 Hz) and mu-beta (15-29 Hz) components. We found that cued attention impacted mu-alpha in the somatotopically localized hand representation in SI, showing decreased power after attention was cued to the hand and increased power after attention was cued to the foot, with significant differences observed 500-1100 milliseconds (ms) post-cue. Mu-beta showed differences in a time window 800–850ms post-cue. The visual cue also drove an early evoked response beginning ~70ms post-cue with distinct peaks modulated with cued attention. Distinct components of the tactile stimulus-evoked response were also modulated with cued attention. Analysis of a second data set showed that, on a trial-by-trial basis, tactile detection probabilities decreased linearly with pre-stimulus mu-alpha and mu-beta power. These results support the growing consensus that cue-induced alpha modulation is a functionally relevant sensory gating mechanism deployed by attention. Further, while cued attention had a weaker effect on the allocation of mu-beta, oscillations in this band also predicted tactile detection.

### Six keywords

magnetoencephalography; sensorimotor; state; attention; beta; rhythm

### Introduction

The historical view of electro-/magneto-encephalography (EEG/MEG) measured alpha rhythms (7-14Hz) as a ‘resting’ brain state is being challenged by evidence that they are actively and topographically deployed to gate information processing. Cued spatial attention leads to decreased alpha amplitudes in parietal-occipital EEG sensors contralateral to the attended site in visual (Worden et al., 2000; Kelly et al., 2006; Thut et al., 2006; Kelly et al., 2009) and inter-sensory visual-auditory tasks (Foxe et al., 1998; Fu et al., 2001). Alpha decreases are accompanied by increases in opposing hemifields and lateralized alpha amplitudes predict reaction times and visual discriminability (Worden et al., 2000; Kelly et

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al., 2006; Thut et al., 2006; Kelly et al., 2009). Recent work has also shown that attentional biases are tied to changes in components of the broad-band cue-induced ER in early visual cortices (Kelly et al., 2009).

In the somatosensory neocortex in humans, a spontaneous mu rhythm containing a complex of mu-alpha (7–14 Hz) and mu-beta (15–29 Hz) components is commonly observed above Rolandic cortex (Tiihonen et al., 1989; Jones et al., 2009). These rhythms show an event related desynchronization (ERD) with stimulation or movement, and in pre-movement periods, with a subsequent synchronization (ERS). There is an increase in alpha-band ERS over the sensorimotor neocortex during visual processing, with a simultaneous alpha ERD over visual cortices, and vice versa during movement (Pfurtscheller, 1992), see also (Rougeul et al., 1979). Further, pre-movement alpha ERD is accentuated in elite athletes over the entire brain, suggesting this is a functionally relevant mechanism that can be enhanced with practice (Del Percio et al., 2009).

Several studies have shown that selective somatic attention impacts movement or sensory induced ERD and ERS changes in sensorimotor mu-alpha and mu-beta activity (Bauer et al., 2006; Babiloni et al., 2008; Dockstader et al., 2010). However, allocation of these rhythms following an attentional cue, in anticipation of tactile sensory processing, has not been investigated.

In the present study, we used MEG imaging to investigate whether similar effects to those observed in the visual system are also present in somatosensation, using the well-localized hand representation in SI as our substrate (Jones et al., 2007; Jones et al., 2009). We investigated whether spatial attention directed to or away from the hand impacted allocation of mu-alpha and mu-beta, the predictive value of these rhythms for detection, and the impact of cued attention on evoked responses. We observed an impact in each of these dimensions, indicating that the decreased expression of localized alpha oscillations could be causally beneficial to attentional regulation employed across neocortical areas.

## Methods

### Subjects

MEG data were collected from 12 neurologically healthy (exclusion criteria included musculoskeletal diseases, arthritis, lupus, multiple sclerosis, scleroderma and diagnosed current psychiatric disorder), right-handed, 18–50 year old adults (mean age=31.6 yrs, s.d.=7 yrs, 1 male and 11 female). Subjects were medication free or on stable doses of SSRI medication. The experimental protocol was approved by the Massachusetts General Hospital Internal Review Board and each subject gave informed consent before data acquisition.

### Stimuli

Subjects' hand and foot rested on solid plastic frames through which tactile stimuli were delivered. The stimulus (single cycle of a 100 Hz sine wave, 10ms duration) was generated by fused multi-layer piezoelectric benders, which provide more favorable force and higher frequency resonance characteristics than typical ceramic wafers (Noliac, Inc., see Jones et al., 2007). Stimuli were applied to the distal pads of the 3<sup>rd</sup> digit of the left hand and 1<sup>st</sup> digit of the left foot via a delrin contactor affixed to the piezoelectric (7 mm diameter presented within a 1 cm circular rigid surround). The device was not glued to the skin. Instead, matched intensity of stimulation, relative to perceptual threshold, was maintained individually for each subject using a Parameter Estimation Sequential Testing (PEST) convergence procedure (Dai, 1995; Leek, 2001). During the cued detection runs described below, stimulus strength was maintained at 66% percent detection threshold with supra-threshold (100% detected) and null-stimuli randomly interleaved for 10% and 20% of the

trials, respectively. The PEST procedure and the hand stimulation device and protocol were as in Jones et al., 2007, 2009.

### Experimental Procedure Localization runs

To aid localization of primary equivalent current dipoles (ECDs) in contralateral SI, each experiment began with presentation of suprathreshold stimuli to the left hand 3<sup>rd</sup> digit for 3 minutes with an ISI of 3 seconds (s); 60 trials per subject. Separate localization runs were also performed on the 1st digit of the foot, as an original goal of our study was to look at the somatotopic precision of attention allocation by comparing hand and foot activity. However, consistent dipoles could not be reconstructed from the foot localization data using the standard ECD localization techniques described below. Thus, only hand area activity is presented, as its precise position in the SI map could be confirmed.

### Cued detection runs

Subjects were instructed to fixate on a cross on a projection screen. PEST procedure was employed for 3 minutes at the beginning to determine subjects' initial detection thresholds. This run was followed by at least 5 cued detection runs, described in Figure 1, consisting of a 3.5s trial that began with the fixation cross changing into a visual word cue on a projection screen directing the participant to attend to either the "Hand" (the *attend in* condition) the "Foot" (the *attend out* condition) or "Either" location. The visual cue was accompanied by a 60dB, 2 kHz tone delivered to both ears to mask audible clicks created by the tactile stimulator and remained constant for 2.5s. At a randomized time between 1.1 and 2.1s (fixed 100ms intervals) after the visual cue, the piezoelectric stimulator delivered a brief tactile stimulus to either the finger or toe. At the end of the 2.5s visual cue, and at least 400ms after tactile stimulus, subjects reported detection or non-detection of the stimulus at the cued location with button presses using the second and third digits of the right hand, respectively. The next trial began 1s after cessation of the visual cue. There were 120 trials per run, 40 of each attention condition totaling at least 200 trials of 3 stimulus strengths in each condition.

### MEG data acquisition and source analysis

The MEG signals were recorded using a 306-channel whole-head planar dc-SQUID Neuromag Vectorview system (Helsinki, Finland). Data were acquired at 601 Hz and filtered from 0.1 to 200 Hz. Four head position coils recorded head position in the Dewar for co-registration with structural MR images. Vertical and horizontal electro-oculogram (EOG) signals were recorded with electrodes placed close to the left eye. Epochs with EOG peak-to-peak amplitude exceeding 100  $\mu$ V were excluded from analysis.

The contribution from the left 3<sup>rd</sup> digit representation in SI to the measured fields was estimated using a least-squares fit with a dipole forward solution calculated using a spherically symmetric conductor model of the head (Hamalainen and Sarvas, 1989). Averaged data from the localization runs described above were used to find an ECD (Elekta-Neuromag, Ltd Helsinki Finland software) at the time of peak activity (mean peak activity = 66.8ms, s.d.= 6.4ms) in the mean signal from the suprathreshold stimuli (minimum n=50 runs per subject). The goodness of fit of this single dipole model was larger than 70% in all fit data during peak responses. Co-registration of the SI source localization with the individual's anatomical MRIs confirmed that the source emerged from the anterior band of the post-central gyrus finger representation of area 3b in SI (Moore et al., 2000) in all subjects (Figure 2A). All analysis considered the forward solution from this SI source.

## Analysis

**Time evolution of spectral power**—This metric was calculated using a complex wavelet analysis, from which time-frequency representations (TFRs) of near instantaneous changes were determined. The TFRs were calculated from 1-40 Hz on the SI ECD time courses by convolving signals with a complex Morlet wavelet of the form

$w(t, f_0) = A \exp(-t^2 / 2\sigma_t^2) \exp(2i\pi f_0 t)$ , for each frequency of interest  $f_0$ , where  $\sigma_t = m / 2\pi f_0$ , and  $i$  is the imaginary unit. The normalization factor was  $A = 1 / (\sigma_t \sqrt{2\pi})$ , and the constant  $m$  defining the compromise between time and frequency resolution was 7, as in (Jones et al., 2009). Time-frequency representations of mu-alpha and mu-beta power were calculated as the squared magnitude of the complex wavelet-transformed data averaged across the range of interest. For the post-cue analysis (Figure 2B), baseline was calculated as averaged power  $[-200, 0]$ ms before the cue - averaged across *attend in* and *attend out* trials separately. For the pre-stimulus analysis (Figure 2C), baseline was calculated as average power  $[-500, 0]$ ms before the stimulus.

Data were analyzed using the last 100 trials of each condition. This choice reflects preliminary analysis across multiple studies in our laboratory (Jones and Moore, unpublished data) indicating that the initial 100 trials provide less stable and consistent neurophysiological activity patterns across individuals.

**Visual cue and tactile stimulus broad-band evoked responses**—SI evoked responses were calculated across an equal number of *attend in* and *attend out* trials per subject from threshold-level tactile stimulation to the finger (number of trials mean=88 trials; s.d.=10). Averages were baseline normalized by subtracting the mean over  $[-100, 0]$ ms from the cue or stimulus, for each subject (Figure 3). A response artifact from 1.7 to 2.1s in one subject was removed from Figure 3A.

**Impact of mu-alpha and mu-beta on detection probabilities**—We could not use the current data to assess the impact of mu-alpha and mu-beta on detection probabilities because the subset of relevant data was a statistically small sample. The relevant data consisted of the ‘hit’ and ‘miss’ trials in the attend hand condition and there were only a small number of miss trials per subject in this sub-condition (number of miss trials: mean=11, s.d.=6; number of hit trials: mean=83, s.d.=11). Therefore, we conducted analysis using a second data set where the statistics were tractable. As in the present study, subjects detected taps applied to the 3<sup>rd</sup> digit fingertip (of the right hand) using the same stimulator, and signals were localized to the hand dipole using identical means. Because foot trials and ‘either’ trials were not interleaved— subjects attended to the hand throughout – we had a more extensive trial base for comparing hit and miss trials (last 100 trials analyzed). Details of data collection were described in detail in prior reports by our group (Jones et al., 2007; Jones et al., 2009; Ziegler et al., 2010).

Analysis methods were as in (Linkenkaer-Hansen et al., 2004). In brief, for each subject mu-alpha and mu-beta power was averaged over a 1s pre-stimulus time window for each of the last 100 threshold-level stimulus trials, and binned into 10 power percentile bins (10 averages per bin) sorted from low to high. The probability of detection in each bin was calculated as a percent change in hit rate (number of detected trials/ total number of trials) from the mean (Figure 4).

**Statistical analyses**—Non-parametric Wilcoxon sign-rank tests were used to assess the statistical significance of differences in *attend in* and *attend out* conditions across subjects at every time point (Figures 2BC and 3). The Wilcoxon test was preferred over ANOVA because the data were non-normally distributed (Shapiro-Wilks test). Linear regression on

the mean percent change in hit rate across subjects was used to assess the impact of mu-alpha and mu-beta power on detection (Figure 4).

## Results

We investigated the temporal evolution of changes in mu-alpha (7-14Hz), and mu-beta (15-29Hz) power in a localized dipole source in the right hand-area of SI after a cue to attend to tactile finger-stimulation to the contralateral left hand (*attend in* condition), or to tactile toe-stimulation to the left foot (*attend out* condition). Figure 2A shows example localizations in two subjects in the SI hand representation in the anterior bank of the postcentral gyrus (area 3b), confirmed by proximity to the omega shaped bend (marked in red Figure 2A bottom panel) in the central sulcus (Moore et al., 2000). Figure 2B shows the corresponding average percent change from baseline ( $n=12$  subjects (Ss)) in SI mu-alpha, and mu-beta power after the cue  $[-100, 1100]$ ms in *attend in* and *attend out* conditions. A significant difference across subjects was observed between the conditions in the mu-alpha band during the anticipatory post-cue time period from  $[500, 1100]$ ms post-cue ( $p<0.05$  marked with asterisks, Wilcoxon sign-rank test). Significant differences in the mu-beta band were observed for a time window between  $[800, 850]$ ms.

Aligning trials to the tactile stimulus onset  $[-1000, 250]$ ms, rather than visual cue, also showed a dominant effect of cued attention on pre-stimulus mu-alpha activity (Figure 2C). Significant differences between *attend in* and *attend out* conditions are seen in the mu-alpha across the entire pre-stimulus time period, and in the  $[-200, 0]$ ms time window for mu-beta, with another period of significance around  $-800$ ms.

Next, we investigated attentional modulation of the broad-band SI evoked response to the visual cue and subsequent threshold-level tactile stimulus (Figure 3). There was a rapid response in SI to the visual cue with an initial peak near 70ms (labeled pcM70, for “post-cue M70”, for reference in Figure 3A) that was greater in the *attend in* condition. Several other time points showed a significant difference in *attend in* vs. *attend out* conditions, and the timings of these differences was consistent with previously reported modulation of EEG measured event-related potentials (ERPs) during attention deployment in parietal, frontal and visual cortices (Kelly et al., 2009). Most notable are the statistically significant differences at 200ms, 400ms and at several intervals between 500–900ms (see magenta asterisks in Figure 3A). The 200ms difference is consistent with that seen in parietal cortices and typically referred to as an ‘early directing-attention negativity’ (EDAN), labeled pcMedan (for “post-cue MEG EDAN”) in Figure 3A. The difference near 400ms is consistent with the anterior directing-attention negativity (ADAN) observed in frontal cortices, and the later non-continuous differences between 500–900ms are in line with those seen over occipital cortex known as late directing-attention positivity (LDAP), labeled pcMadan and pcMldap, respectively.

Figure 3B shows the SI tactile ER from  $[-100, 175]$ ms. Peaks in the waveform were consistent with previous reports using similar stimuli (Jones et al., 2007; Jones et al., 2009). Four peaks occurring at approximately 50ms (M50), 70ms (M70), 100ms (M100), and 135ms (M135), respectively, are labeled for visualization as in (Jones et al., 2007; Jones et al., 2009). A previous study showed that high pre-stimulus mu-alpha and mu-beta was correlated with an increase in the magnitude of the M50 peak and a subsequent trend toward decreased M70 and later response elements (Jones et al., 2009). Here, we found that there was also a significant difference in the magnitude of the ER near the M50 peak between the *attend in* versus *attend out* conditions, such that the magnitude of the ER was greater in the *attend out* conditions, when pre-stimulus mu-alpha and mu-beta were higher (Figure 3B,



significant time-points marked with asterisks,  $p < 0.05$  Wilcoxon sign-rank test). There was also a significant difference in the ER near the M100 peak ( $p < 0.05$  Wilcoxon sign-rank).

Although a slow cue-locked fluctuation is apparent visually in the averaged cue ER in *attend in* and *attend out* conditions (Figure 3A), this did not bias the averaged tactile ER (Figure 3B) since the tactile stimulus was jittered within the [1.1, 2.1]s post-cue time window (marked in Figure 3A). However, it is possible this early ER was impacted by post-cue attentional modulation of the mu-alpha and mu-beta activity that is not phase-locked to the cue (Figure 2) (see **Discussion**).

We assessed trial-by-trial impact of pre-stimulus mu-alpha and mu-beta in our SI signal on tactile detection probabilities, using a second data set that employed analogous MEG and tactile detection methods, but with sustained attention to the finger, (Jones et al., 2007; Jones et al., 2009; Ziegler et al., 2010). This previously collected data set gave greater statistical power than the current data, where the relevant hit and miss trials represented a statistically small sample (see **Methods**). Following prior convention (Linkenkaer-Hansen et al., 2004), on individual trials average pre-stimulus mu-alpha and mu-beta power was calculated (1s pre-stimulus) and sorted from high to low power into 10 equally sized percentile bins. Detection probabilities in each bin were calculated as the percent change in hit rate from the mean (see **Methods**). We found a linear relationship between tactile detection probabilities and mu-alpha and mu-beta power ( $p < 0.05$ , F-test,  $R^2 = 0.65$  and  $R^2 = 0.85$ , respectively) such that the hit probability was greater during trials with lower pre-stimulus mu-alpha and mu-beta power (Figure 4).

## Discussion

Consistent with findings in visual cortices, we observed that cued attention modulates anticipatory post-cue mu-alpha activity and early peaks in the broad-band visual cue and tactile stimulus induced ERs in the SI hand representation. We found a significant difference in the post-cue change from baseline of mu-alpha power between *attend in* and *attend out* conditions. Detection probabilities were greater during lower pre-stimulus mu-alpha and mu-beta power. These results are consistent with the theory that attentionally induced focal alpha changes are an active mechanism for modulation of sensory information processing (Foxe et al., 1998; Worden et al., 2000; Kelly et al., 2006; Thut et al., 2006; Klimesch et al., 2007; Kelly et al., 2009). Further, our results show that although attentional cueing has a weaker impact on SI mu-beta rhythms, they also predict tactile detection.

### Attentional modulation of low frequency rhythms and their impact on perception

Prior research connecting low frequency oscillations and cued attention in somatosensory cortex in humans has focused on sensory-stimulus and movement induced ERD and subsequent ERS in alpha and beta frequencies (Bauer et al., 2006; Babiloni et al., 2008; Dockstader et al., 2010), see also (Pfurtscheller, 1992). These studies also investigated attentional modulation of somatosensory gamma (35–80 Hz) activity. Gamma was not a focus of our study because it is not robust in our spontaneous SI signal (see Jones et al., 2009).

Our finding of a linear relationship between mu-alpha and mu-beta power and tactile detection agrees with (Schubert et al., 2008a), which found a linear relationship between alpha and beta amplitudes in EEG electrodes over SI and tactile detection probability. These results also are consistent with the relationship between smaller alpha amplitudes and increased perception and decreased reaction times in the visual system (Thut et al., 2006; Hanslmayr et al., 2007; van Dijk et al., 2008; Kelly et al., 2009). Other studies in the somatosensory (Linkenkaer-Hansen et al., 2004; Zhang and Ding, 2009) and visual systems

(Rajagovindan and Ding), have reported an inverted-U relationship between alpha power and detection probabilities. We also found that, on trials with the lowest values of mu-alpha power, detection probability diminished compared to slightly higher values (compare 10<sup>th</sup> and 20<sup>th</sup> percentiles in Figure 4), suggesting that a minimal baseline of alpha activity is necessary for optimal signal propagation. These results imply that the reduction of mu-alpha and mu-beta activity in SI with cued attention is an active cortical gating mechanism that increases the perceptual salience of tactile signals.

### Attentional modulation of visual cue and tactile stimulus SI ERs

Studies have shown consistent effects regarding the timing and spatial specificity of distinct components of post-cue EEG measured ERPs in parietal, frontal and low-level visual areas (e.g. Kelly et al., 2009). We have shown that attentional modulation of broad-band visual cue induced ERs components exists at similar times in our high-resolution localized SI signal. In addition to changes near 200ms (pcMedan), 400ms (pcMadan), and between 500–900ms activity (pcMldap), we found an earlier significant difference at ~70ms (pcM70), such that the magnitude of the peak was greater in *attend in* conditions (Figure 3A), suggesting rapid attentional modulation in SI.

While fitting data to a single dipole is a necessary simplification in our study, the pcM70 response difference is likely restricted to activity from SI. Rapid responses (<100ms) to visual stimuli have been observed previously in SI. Zhou and Fuster (1997 in SI. Zhou and Fuster (2001) showed a change in firing rate (predominantly increases) in single units in the anterior parietal cortex of trained monkeys, including the hand representation area in SI, during a visual cue indicating a subsequent tactile choice. In this visuo-haptic memory task, a change in firing rate was observed as early as ~50–100ms post-visual-cue and lasted throughout a memory retention period (~20s). Further, some units showed differential activity depending on haptic choice indicated by the cue—vertical or horizontal bars indicating corresponding rod with oriented ridges to pull (Zhou and Fuster, 1997, 2000).

Our findings of increased magnitude near the M50 and M100 SI tactile ER peaks (Figure 3B) with attention are consistent with the theory that attention increases the gain of sensory evoked responses, and are in line with previous studies that showed increased magnitudes of evoked SI activity in MEG/EEG sensor data at similar time points (Schubert et al., 2008b; Dockstader et al., 2010). However, the decreased M50 peak in the *attend in* condition contrasts with previous studies showing increases near 50ms with attention (Iguchi et al., 2002; Schubert et al., 2008b; Dockstader et al., 2010). These discrepancies are likely due to differences in experimental design and the fact that the previous studies used stimuli that were perceptually salient (electrical and Braille stimuli), in contrast to our stimulus amplitude that was maintained at a 50% perceptual threshold. The ~50ms differences in Iguchi et al. (2002) appeared during a two-finger discrimination task, but not during a non-discrimination task. Schubert et al. (2008b) employed an oddball detection paradigm, and Dockstader et al. (2010) engaged attention by counting stimuli. Further, the relative magnitude of evoked activity in SI can vary as a function of context, with identical stimuli causing enhanced or suppressed responses dependent on the amplitude of sensory drive (Moore et al., 1999). In our study, greater pre-stimulus mu activity may similarly prime the enhancement of this early response component under conditions of weak sensory drive.

### Biophysical mechanisms of SI attentional modulation: Connection to previous computational modeling predictions

**SI Mu-Alpha Rhythms**—We have developed a model of SI that predicts the origin of the MEG mu rhythm and tactile ERs (Jones et al., 2007; Jones et al., 2009). The model predicts that the mu-alpha component of the mu rhythm is created by a 10Hz lemniscal thalamic

input to granular and infragranular layers, while the mu-beta component is dependent on a second 10Hz input to the supragranular layers. Given our model, the observed attentional decrease of mu-alpha is predicted to occur through suppression of ongoing 10Hz lemniscal thalamus activity. This is consistent with the notion proposed by Francis Crick that the inhibitory reticular thalamus controls an attentional “searchlight” in topographic sensory representations (Crick, 1984) and recent recordings by (McAlonan et al., 2008) showing attention modulates sensory evoked thalamic responses before reaching the neocortex (see also (Suffczynski et al., 2001)).

**SI ERs**—Our previous modeling further predicts that the decreased M50 tactile stimulus peak responses with attention may arise, at least in part, from excitatory neurons that are less depolarized during low pre-stimulus mu and hence have a smaller immediate post-stimulus (M50) response. This decreased excitatory response leads to decreased post-stimulus inhibition in the network, which enables greater subsequent M70 and M100 responses (see Jones et al., 2009). Recent research suggests that alpha rhythms may be amplified by a recruitment of a class of low-threshold spiking inhibitory neurons (Fanselow et al., 2008; Vierling-Claassen et al., In Review). These predictions provide a direct neural correlate for the theory that mu-alpha exerts inhibitory control in the neocortex (Worden et al., 2000; Klimesch et al., 2007).

Further, the negative polarity of the post-cue SI pcM70 suggests it was driven by excitatory input to the supragranular layers, from higher order neocortical or non-specific thalamic sources (Jones et al., 2007). A subsequent peak with negative polarity emerges ~100ms later, reflective of a 2-cycle cue-locked ~10Hz drive, which is stronger with attention. The attentional differences between 500–900ms (pcM1dap) appear to be tied to the cue-locked slow fluctuation. Slow oscillations are known to modulate higher frequency rhythms (Schroeder and Lakatos, 2009), however an investigation of this is beyond the scope of this study.

In summary, our results support the idea that alpha deployment may be a general mechanism of cued-attention for active sensory gating. Mu-beta rhythms are impacted less by attentional cueing, but are well correlated with the probability of tactile detection. This dissociation suggests that while both oscillations impact signal processing, mu-alpha deployment may be more readily recruited during attentional allocation. Future research is needed to identify if attentional mu-alpha modulation is somatotopically precise on finer spatial scales, as has been explored in the visual system.

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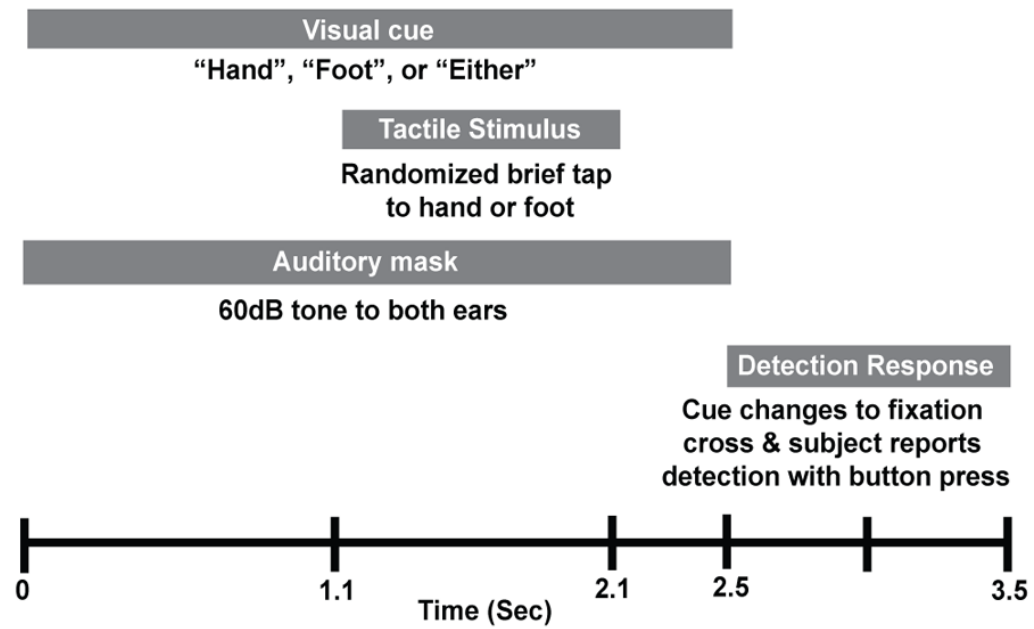
## References

- Babiloni C, Capotosto P, Brancucci A, Del Percio C, Petrini L, Buttiglione M, Cibelli G, Romani GL, Rossini PM, Arendt-Nielsen L. Cortical alpha rhythms are related to the anticipation of sensorimotor interaction between painful stimuli and movements: a high-resolution EEG study. *J Pain*. 2008; 9:902–911. [PubMed: 18619907]
- Bauer M, Oostenveld R, Peeters M, Fries P. Tactile spatial attention enhances gamma-band activity in somatosensory cortex and reduces low-frequency activity in parieto-occipital areas. *J Neurosci*. 2006; 26:490–501. [PubMed: 16407546]

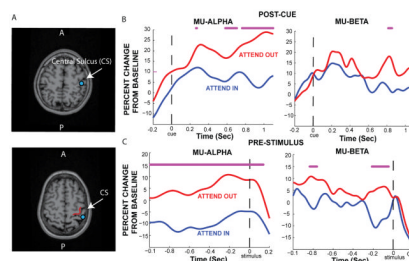


- Crick F. Function of the thalamic reticular complex: the searchlight hypothesis. *Proc Natl Acad Sci U S A*. 1984; 81:4586–4590. [PubMed: 6589612]
- Dai H. On measuring psychometric functions: a comparison of the constant-stimulus and adaptive up-down methods. *J Acoust Soc Am*. 1995; 98:3135–3139. [PubMed: 8550938]
- Del Percio C, Babiloni C, Bertollo M, Marzano N, Iacoboni M, Infarinato F, Lizio R, Stocchi M, Robazza C, Cibelli G, Comani S, Eusebi F. Visuo-attentional and sensorimotor alpha rhythms are related to visuo-motor performance in athletes. *Hum Brain Mapp*. 2009; 30:3527–3540. [PubMed: 19350556]
- Dockstader C, Cheyne D, Tannock R. Cortical dynamics of selective attention to somatosensory events. *Neuroimage*. 2010; 49:1777–1785. [PubMed: 19781649]
- Fanselow EE, Richardson KA, Connors BW. Selective, state-dependent activation of somatostatin-expressing inhibitory interneurons in mouse neocortex. *J Neurophysiol*. 2008; 100:2640–2652. [PubMed: 18799598]
- Foxe JJ, Simpson GV, Ahlfors SP. Parieto-occipital approximately 10 Hz activity reflects anticipatory state of visual attention mechanisms. *Neuroreport*. 1998; 9:3929–3933. [PubMed: 9875731]
- Fu KM, Foxe JJ, Murray MM, Higgins BA, Javitt DC, Schroeder CE. 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*. 2001; 12:145–152. [PubMed: 11489617]
- Hamalainen MS, Sarvas J. Realistic conductivity geometry model of the human head for interpretation of neuromagnetic data. *IEEE Trans Biomed Eng*. 1989; 36:165–171. [PubMed: 2917762]
- Hanslmayr S, Aslan A, Staudigl T, Klimesch W, Herrmann CS, Bauml KH. Prestimulus oscillations predict visual perception performance between and within subjects. *Neuroimage*. 2007; 37:1465–1473. [PubMed: 17706433]
- Hughes SW, Crunelli V. Thalamic mechanisms of EEG alpha rhythms and their pathological implications. *Neuroscientist*. 2005; 11:357–372. [PubMed: 16061522]
- Iguchi Y, Hoshi Y, Tanosaki M, Taira M, Hashimoto I. Selective attention regulates spatial and intensity information processing in the human primary somatosensory cortex. *Neuroreport*. 2002; 13:2335–2339. [PubMed: 12488822]
- Jones SR, Pritchett DL, Stufflebeam SM, Hamalainen M, Moore CI. Neural Correlates of Tactile Detection: A Combined MEG and Biophysically Based Computational Modeling Study. *Journal of Neuroscience*. 2007; 27:10751–10764. [PubMed: 17913909]
- Jones SR, Pritchett DL, Sikora MA, Stufflebeam SM, Hamalainen M, Moore CI. Quantitative analysis and biophysically realistic neural modeling of the MEG mu rhythm: rhythmogenesis and modulation of sensory-evoked responses. *J Neurophysiol*. 2009; 102:3554–3572. [PubMed: 19812290]
- Kelly SP, Gomez-Ramirez M, Foxe JJ. The strength of anticipatory spatial biasing predicts target discrimination at attended locations: a high-density EEG study. *Eur J Neurosci*. 2009; 30:2224–2234. [PubMed: 19930401]
- Kelly SP, Lalor EC, Reilly RB, Foxe JJ. Increases in alpha oscillatory power reflect an active retinotopic mechanism for distracter suppression during sustained visuospatial attention. *J Neurophysiol*. 2006; 95:3844–3851. [PubMed: 16571739]
- Klimesch W, Sauseng P, Hanslmayr S. EEG alpha oscillations: the inhibition-timing hypothesis. *Brain Res Rev*. 2007; 53:63–88. [PubMed: 16887192]
- Leek MR. Adaptive procedures in psychophysical research. *Percept Psychophys*. 2001; 63:1279–1292. [PubMed: 11800457]
- Linkenkaer-Hansen K, Nikulin VV, Palva S, Ilmoniemi RJ, Palva JM. Prestimulus oscillations enhance psychophysical performance in humans. *J Neurosci*. 2004; 24:10186–10190. [PubMed: 15537890]
- McAlonan K, Cavanaugh J, Wurtz RH. Guarding the gateway to cortex with attention in visual thalamus. *Nature*. 2008; 456:391–394. [PubMed: 18849967]
- Moore CI, Nelson SB, Sur M. Dynamics of neuronal processing in rat somatosensory cortex. *Trends Neurosci*. 1999; 22:513–520. [PubMed: 10529819]

- Moore CI, Stern CE, Corkin S, Fischl B, Gray AC, Rosen BR, Dale AM. Segregation of somatosensory activation in the human rolandic cortex using fMRI. *J Neurophysiol.* 2000; 84:558–569. [PubMed: 10899227]
- Pfurtscheller G. Event-related synchronization (ERS): an electrophysiological correlate of cortical areas at rest. *Electroencephalogr Clin Neurophysiol.* 1992; 83:62–69. [PubMed: 1376667]
- Rajagovindan R, Ding M. From Prestimulus Alpha Oscillation to Visual-evoked Response: An Inverted- U Function and Its Attentional Modulation. *J Cogn Neurosci.*
- Rougeul A, Bouyer JJ, Dedet L, Debray O. Fast somato-parietal rhythms during combined focal attention and immobility in baboon and squirrel monkey. *Electroencephalogr Clin Neurophysiol.* 1979; 46:310–319. [PubMed: 85524]
- Schroeder CE, Lakatos P. Low-frequency neuronal oscillations as instruments of sensory selection. *Trends Neurosci.* 2009; 32:9–18. [PubMed: 19012975]
- Schubert R, Haufe S, Blankenburg F, Villringer A, Curio G. Now You'll Feel It-Now You Won't: EEG Rhythms Predict the Effectiveness of Perceptual Masking. *J Cogn Neurosci.* 2008a
- Schubert R, Ritter P, Wustenberg T, Preuschhof C, Curio G, Sommer W, Villringer A. Spatial attention related SEP amplitude modulations covary with BOLD signal in S1--a simultaneous EEG--fMRI study. *Cereb Cortex.* 2008b; 18:2686–2700. [PubMed: 18372293]
- Suffczynski P, Kalitzin S, Pfurtscheller G, Lopes da Silva FH. Computational model of thalamo-cortical networks: dynamical control of alpha rhythms in relation to focal attention. *Int J Psychophysiol.* 2001; 43:25–40. [PubMed: 11742683]
- Thut G, Nietzel A, Brandt SA, Pascual-Leone A. Alpha-band electroencephalographic activity over occipital cortex indexes visuospatial attention bias and predicts visual target detection. *J Neurosci.* 2006; 26:9494–9502. [PubMed: 16971533]
- Tiihonen J, Kajola M, Hari R. Magnetic mu rhythm in man. *Neuroscience.* 1989; 32:793–800. [PubMed: 2601846]
- van Dijk H, Schoffelen JM, Oostenveld R, Jensen O. Prestimulus oscillatory activity in the alpha band predicts visual discrimination ability. *J Neurosci.* 2008; 28:1816–1823. [PubMed: 18287498]
- Vierling-Claassen D, Cardin J, Moore C, Jones SR. Computational modeling of distinct neocortical oscillations driven by cell-type selective optogenetic drive: Separable resonant circuits controlled by low-threshold spiking and fast-spiking interneurons. *Frontiers in Neuroscience Special Issue: Origin and Consequences of Rhythmic Activity.* (In Review).
- Worden MS, Foxe JJ, Wang N, Simpson GV. Anticipatory biasing of visuospatial attention indexed by retinotopically specific alpha-band electroencephalography increases over occipital cortex. *J Neurosci.* 2000; 20:RC63. [PubMed: 10704517]
- Zhang Y, Ding M. Detection of a Weak Somatosensory Stimulus: Role of the Prestimulus Mu Rhythm and Its Top-Down Modulation. *J Cogn Neurosci.* 2009
- Zhou YD, Fuster JM. Neuronal activity of somatosensory cortex in a cross-modal (visuo-haptic) memory task. *Exp Brain Res.* 1997; 116:551–555. [PubMed: 9372304]
- Zhou YD, Fuster JM. Visuo-tactile cross-modal associations in cortical somatosensory cells. *Proc Natl Acad Sci U S A.* 2000; 97:9777–9782. [PubMed: 10944237]
- Ziegler DA, Pritchett DL, Hosseini-Varnamkhasti P, Corkin S, Hamalainen M, Moore CI, Jones SR. Transformations in oscillatory activity and evoked responses in primary somatosensory cortex in middle age: A combined computational neural modeling and MEG study. *Neuroimage Epub.* 2010

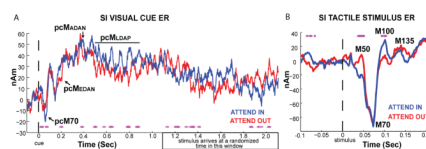


**Figure 1.**  
Experimental design for cued detection runs.  
See **Methods**.



**Figure 2. Impact of cued attention on SI mu-alpha and mu-beta**

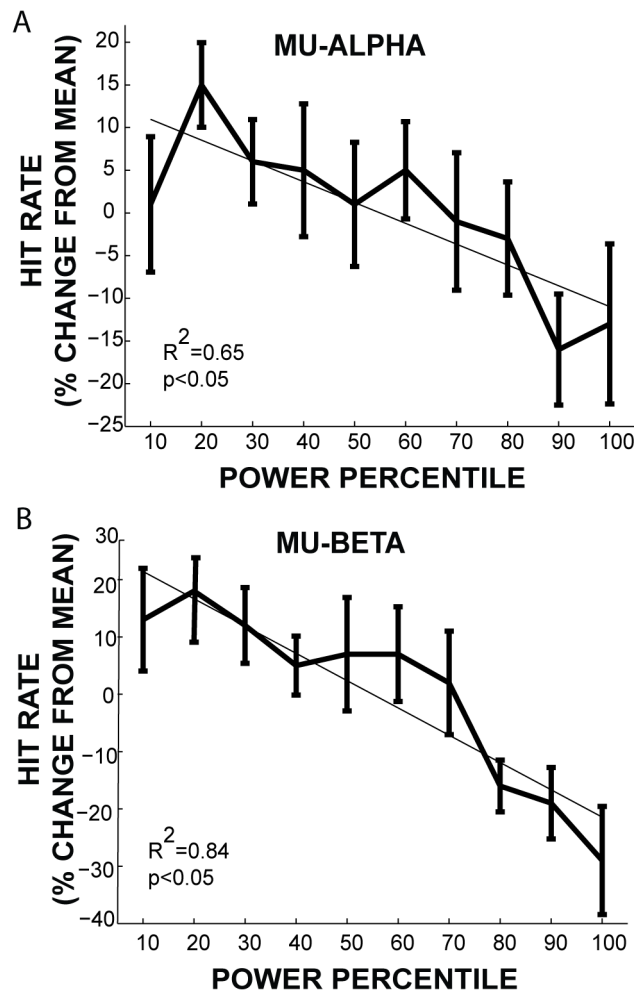
**A** Two examples of the estimated SI ECD localizations (blue dots) overlaid on the subjects' structural MRI brain images. Response evoked by a suprathreshold tactile stimulus to the left hand, third digit, was localized to the SI hand representation in area 3b, confirmed by proximity to the omega shape (marked in red bottom panel), in the anterior bank of the contralateral post-central gyrus. **B** Continuous post-cue temporal evolution of the hand area SI mu-alpha (7–14Hz), and mu-beta (15–29Hz) activity in *attend in* and *attend out* conditions (avg. n=12Ss). **C** Corresponding continuous pre-stimulus evolution of mu-alpha mu-beta. (Asterisks: significant difference between conditions  $p < 0.05$ ).



**Figure 3. Impact of cued attention visual cue and tactile stimulus SI ERs**

**A** Average hand area SI broad-band ER from the visual cue in *attend in* and *attend out* conditions (mean  $n=12$  Ss). **B** Corresponding average SI broad-band ER from subsequent threshold-level tactile stimulation to the hand in *attend in* and *attend out* conditions. (Asterisks: significant difference between conditions  $p<0.05$ ).





**Figure 4. Impact of pre-stimulus mu-alpha and mu-beta power on detection probabilities**  
**A** Tactile detection probabilities, measured as percent change in hit rate from the mean, as a function mu-alpha power sorted into 10 power percentile bins. Bold traces: mean and standard error across subjects ( $n=10$ Ss), Thin traces: Linear fit from linear regression analysis ( $R^2=0.65$ ,  $p<0.05$ ). **B** Analogous traces as a function of mu-beta power ( $R^2=0.84$ ,  $p<0.05$ ). This analysis was performed on data in Jones et al., 2007,<sup>2009</sup> (see **Methods**).