


Pre-stimulus alpha oscillation and post-stimulus cortical activity differ in localization between consciously perceived and missed near-threshold somatosensory stimuli

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Funding information

Japan Society for the Promotion of Science, Grant/Award Numbers: 17K01499, 20K11154

Edited by: Ali Mazaheri

Abstract

Conscious perception of a near-threshold (NT) stimulus is characterized by the pre- and post-stimulus brain state. However, the power of pre-stimulus neural oscillations and strength of post-stimulus cortical activity that lead to conscious perception have rarely been examined in individual cortical areas. This is because most previous electro- and magnetoencephalography (EEG and MEG, respectively) studies involved scalp- and sensor-level analyses. Therefore, we recorded MEG during a continuous NT somatosensory stimulus detection task and applied the reconstructed source data in order to identify cortical areas where the post-stimulus cortical activity and pre-stimulus alpha oscillation predict the conscious perception of NT somatosensory stimuli. We found that the somatosensory hierarchical processing areas, prefrontal areas and cortical areas belonging to the default mode network showed stronger cortical activity for consciously perceived trials in the post-stimulus period, but the cortical activity in primary somatosensory area (SI) is independent of conscious perception during the early stage of NT stimulus processing. In addition, we revealed that the pre-stimulus alpha oscillation only in SI is predictive of conscious perception. These findings suggest that the bottom-up stream of somatosensory information flow following SI and pre-stimulus alpha activity fluctuation in SI as a top-down modulation are crucial constituents of conscious perception.

KEYWORDS

conscious, magnetoencephalography, near-threshold, perception, somatosensory

Abbreviations: ACC, anterior cingulate cortex; CAL, calcarine sulcus; DMN, default mode network; ECG, electrocardiogram; EEG, electroencephalography; EOG, electro-ocular gram; FDR, false discovery rate; GLMM, generalized linear mixed-effects model; iFC, inferior frontal cortex; iPC, inferior parietal cortex; iTG, inferior temporal gyrus; IOFC, lateral orbitofrontal cortex; MEG, magnetoencephalography; mOFC, medial orbitofrontal cortex; NT, near-threshold; parHip, parahippocampus; pCS, postcentral sulcus; POS, parieto-occipital sulcus; ROIs, regions of interest; SI, primary somatosensory area; SII, secondary somatosensory area; sTG/mTG, superior/middle temporal gyrus.

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1 | INTRODUCTION

Conscious perception of a near-threshold (NT) somatosensory stimulus is characterized by the pre- and post-stimulus brain state. Many studies have been conducted on these brain states regarding post-stimulus local cortical excitability and pre-stimulus neuronal oscillation (Auksztulewicz et al., 2012; Baumgarten et al., 2016; Hanslmayr et al., 2007; Iemi et al., 2017; Jones et al., 2010; Lange et al., 2012; Nierhaus et al., 2015; Weisz et al., 2014; Wittenberg et al., 2018). In the pre-stimulus period, a lower alpha oscillation power in task-relevant areas leads to more reports of perceived stimuli, even in the absence of actual stimuli (Baumgarten et al., 2016; Frey et al., 2016; Jones et al., 2010; Lange et al., 2012; Weisz et al., 2014; Wittenberg et al., 2018). These observations can usually be explained by the suggestion that alpha activity reflects cortical excitability with strong alpha oscillation indicating functional inhibition (alpha inhibition hypothesis) (Jensen & Mazaheri, 2010; Klimesch et al., 2007). A series of information processing of NT somatosensory stimuli is not constant or fixed but fluctuates due to nonstationary alpha power in the pre-stimulus period (Baumgarten et al., 2016; Jones et al., 2010; Schubert et al., 2009; Wittenberg et al., 2018, but see Lange et al., 2012). These studies primarily examined alpha power in the primary somatosensory area (SI) and reported that the perceptual performance is negatively correlated with the pre-stimulus alpha power in SI.

In addition to pre-stimulus neuronal oscillation, the post-stimulus cortical activity also predicts the conscious perception of NT somatosensory stimuli (Auksztulewicz et al., 2012; Boly et al., 2007; Linkenkaer-Hansen et al., 2004; Nierhaus et al., 2015; Palva et al., 2005; Zhang & Ding, 2010). The strength of evoked cortical activity is positively correlated with conscious perception (Auksztulewicz et al., 2012; Linkenkaer-Hansen et al., 2004; Nierhaus et al., 2015; Palva et al., 2005; Zhang & Ding, 2010). A magnetoencephalography (MEG) source-level analysis study revealed that not only somatosensory-related areas (SI and the secondary somatosensory area [SII]) but also prefrontal cortex, known to be involved in higher level cognitive processes and attentional control, predicted conscious perception of NT stimuli (Hirvonen & Palva, 2016). Similarly, a functional magnetic resonance imaging (MRI) study assessing NT somatosensory perception revealed that the prefrontal, superior parietal and anterior cingulate cortex (ACC) are involved in conscious perception (Boly et al., 2007). These previous studies suggest that neuronal activity in prefrontal cortices, which may vary in terms of spatial and time distribution depending on the sensory modality of stimuli, may contribute to somatosensory

awareness, even though this contribution might be indirect via other brain regions under the influence of prefrontal cortices (Dehaene & Changeux, 2011).

Regarding the temporal dynamics of neural activity elicited by NT stimuli, scalp-level electroencephalography (EEG) and sensor-level MEG studies using sub-threshold stimulation revealed that the early component at ~60 ms (P60 or M60 and M70 in Jones et al., 2007) in SI was observed independent of conscious perception and that there was no subsequent component in unperceived trials (Auksztulewicz et al., 2012; Jones et al., 2007; Linkenkaer-Hansen et al., 2004; Nierhaus et al., 2015; Zhang & Ding, 2010), which suggests that the early processing steps in SI, which is an indicator of early entry of stimuli to consciousness, is not a sufficient condition for conscious perception of NT somatosensory stimuli. In line with this, MEG studies emphasized the importance of the later stages of the processing pathway, that is, recurrent neural processing between SI and SII and the long-lasting activity in SII, respectively, on conscious perception (Auksztulewicz et al., 2012; Wühle et al., 2010, 2011). These findings also suggest the late entry of NT stimuli to consciousness. On the other hand, contrary to the importance of the later stage in conscious perception, some previous studies reported that a difference due to conscious perception occurred during the early response in SI (Hirvonen & Palva, 2016; Jones et al., 2007; Palva et al., 2005). Hirvonen and Palva (2016) conducted detailed temporal and spatial analyses in their source analysis using MEG, but their results differ from those of the previous studies mentioned above in terms of physiological engaging mechanisms of SI in conscious perception of NT somatosensory stimuli. This discrepancy indicates that the involvement of the somatosensory-related cortical area in conscious perception is still not fully understood (Wühle et al., 2010). A reason for the insufficient consideration is that most previous EEG and MEG studies applied sensor- and scalp-level analyses to investigate conscious perception of NT somatosensory stimuli. To our knowledge, MEG studies using reconstructed data in the somatosensory domain have not been sufficiently conducted, with the report of Hirvonen and Palva (2016) being the sole literature. In addition, the relationship between perceptual performance and pre-stimulus alpha power has not been clarified for brain regions other than SI and SII, because the previous studies on pre-stimulus alpha power mentioned above used scalp-level or sensor-level analysis methods. It remains unclear whether the activity in higher somatosensory-related areas and prefrontal regions associated with recurrent processing is directly affected by pre-stimulus alpha power fluctuation or indirectly by the influence of upstream brain regions.

The purposes of this study were (1) to examine whether the post-stimulus early component in SI is observed independent of conscious perception, (2) to reveal the brain regions showing enhanced cortical activity following the NT stimulus in the whole brain, and (3) to examine whether the pre-stimulus alpha frequency power in the brain region with enhanced cortical activity following the NT stimulus is decreased. The first aim will help clarify the physiological involvement of SI in conscious perception of NT somatosensory stimuli, especially early processing steps. The second is a replicate investigation of brain regions involved in early processing and recurrent neural processing using source analysis. In addition, the third will help clarify the effect of alpha power fluctuation, which is to some extent detached from early processing steps and recurrent neural processing.

To this end, we recorded MEG during a continuous NT stimulus detection task and used reconstructed source data that allow us to hypothesize on underlying source locations, which is difficult in sensor- and scalp-level analyses. We firstly examined the cortical areas with a difference in the strength of cortical activity between consciously perceived and unperceived trials and, then, related to cortical areas with significant differences, explored whether there is a significant difference in alpha oscillation power in the pre-stimulus period.

2 | METHODS

2.1 | Participants

Nineteen healthy volunteers (11 males, mean age: 22.1 ± 1.1) participated in this experiment. All participants showed right-hand dominance as assessed by the Edinburgh Handedness Questionnaire (Oldfield, 1971), and they did not report any history of neurological or orthopaedic disease resulting in sensory disturbance. Each participant gave informed consent for the study and experimental protocol prior to commencement. This study was approved by the ethical committee of the Faculty of Medicine, Nagoya University (approval number: 2018-0111-2) and conducted in accordance with the Declaration of Helsinki.

2.2 | Experimental protocol

We used a continuous threshold-stimulus detection task whose electrical stimuli were presented with an intensity at the threshold of detection (Hirvonen & Palva, 2016; Zhang & Ding, 2010). Participants received electrical stimuli applied by a pair of ring electrodes placed

between the two distal joints of the right index finger. A 0.5-ms constant-current square-wave electrical pulse was delivered to the electrodes using an electrical stimulator (SEN-3401, Nihon Kohden, Japan). The intensity of the stimuli was set to each individual's sensory threshold level (mean: 1.6 ± 0.5 mA). Before measurement, ascending and descending series of stimulus intensities were delivered until participants began to feel the stimulus in ascending series or did not feel the stimulus presented in descending series. The threshold for each participant was defined as the average of the transition points from both series (Ai & Ro, 2014). The interstimulus interval was pseudo-randomly set from 2.5 to 3.0 s to include cortical activity of SII in an investigation and avoid habituation of the SII response (Kakigi et al., 2000; Wikström et al., 1996). To avoid participant's anticipation, one out of three stimulations was randomly omitted from a series of stimuli. Three hundred NT stimuli were presented, divided into three sessions (7 min each) with a short break. During the recording, the fixation point was always presented in the middle of a screen 30 cm in front of the participants. They were instructed to press a button in their left hand when they perceived the electrical stimulus, while looking at the fixation point. No feedback on whether the response was correct was given to the participants during recording (Frey et al., 2016; Leske et al., 2015).

2.3 | Data recordings

We used a 160-channel MEG system (axial-type first-order gradiometers; PQ1160C, RICOH, Japan) with a sampling rate of 5000 Hz. The magnetically shielded room used during MEG recording has a three-layer design consisting of an aluminium shell with one layer of soft magnetic material (Mumetal) with high permeability on each side of the aluminium. The initial bandpass filter was between 0.3 and 2000 Hz, with a notch filter at 60 Hz. An electro-ocular gram (EOG) and an electrocardiogram (ECG) were simultaneously recorded for artefact rejection in the pre-processing stage. MEG signals were continuously collected for 420 s per session. Prior to the MEG recording in each participant, their scalp shape was digitally traced (SR system-R, Yokogawa, Japan) to fit the MEG coordinates to those of the standardized brain.

2.4 | Behavioural performance

To avoid contamination of the behavioural response into the analysis time window in the pre-stimulus period

(≥ -1500 ms from stimulus onset), a trial followed by a correct response 0.1–1.0 s after the onset was categorized as consciously perceived (Hit), and no response was categorized as unperceived (Miss). The hit rate was the number of correct responses as a percentage of all presented stimuli, and the false response rate was the number of incorrect responses expressed as the same percentage.

To examine whether the perceived trial is affected by the preceding stimulus type and session, we applied two-way repeated measures analysis of variance (ANOVA) (three preceding stimulus types [perceived, unperceived and omitted stimulus] \times 3 sessions).

2.5 | MEG data analysis

We used Brainstorm for all MEG data analyses including preprocessing, source-level analysis and estimation of a time-frequency map (Tadel et al., 2011) (<http://neuroimage.usc.edu/brainstorm/>).

First, the raw MEG time series were downsampled to 300 Hz. Then, we detected artefacts caused by the heartbeat and eye blink on referring to simultaneous recordings of EOG and ECG and automatically removed them using signal-space projections (Nolte & Curio, 1999). Furthermore, segments with residual artefacts of extra-cephalic origin were identified and excluded by visual inspection from datasets before further analysis. For all further analyses, an equal number of hit and miss trials was randomly selected to prevent any bias across conditions (mean trial number: 116.6 ± 22.6) (Frey et al., 2016). These trials were subsequently analysed separately from each other. The preprocessed MEG time series were subsequently epoched into trials of -1500 to 500 ms from stimulus onset. Then, we computed individual MEG forward models using the overlapping-sphere method and reconstructed source imaging using the depth-weighted minimum norm model (Hämäläinen & Ilmoniemi, 1994) and obtained a set of elementary current dipoles, up to 7500 dipoles, distributed over the individual cortical envelope. Each individual cortical envelope was created by warping the default brain anatomy in Brainstorm, ICBM152, based on each individual digitized head shape, labelled with Freesurfer/Destrieux. The default analysis pipeline in FreeSurfer implements an automatic parcellation of the cortical surface in anatomical regions. One of them is the Destrieux cortical atlas, which provides 148 sulco-gyral structures in both hemispheres (Destrieux et al., 2010). We set 148 regions of interest (ROIs) based on the Destrieux atlas in this study.

2.5.1 | Post-stimulus neuronal activity

For each participant, the MEG source signals were averaged across trials and z-scored based on the baseline (-100 to 0 ms) before group-level statistical tests between hit and miss. For the analysis of temporal dynamics, time series of averaged source signals in SI and SII were extracted for each participant. In this study, we recognized two ROIs in Destrieux: G_postcentral and G_and_S_subcentral as SI and SII, respectively. We estimated the significant time-series components against the baseline in contralateral SI and SII, respectively, for each condition. To investigate the significant time-series components, we used a one-sample parametric *t* test against the baseline, while correcting for multiple comparisons using the false discovery rate (FDR) method (Benjamini & Hochberg, 1995) over the time dimension to control for the expected proportion of false positives. The significant differences between hit and miss conditions in the time-series components and the reconstructed source map were estimated with the parametric paired *t* test (Morillon & Baillet, 2017), with FDR over the dimensions of time, and source signals and time, respectively.

2.5.2 | Pre-stimulus time frequency

To transform data into time-frequency domains, Morlet wavelets were applied to single trial source time series in 20 ROIs separately, which included the brain regions showing significant differences in the strength of cortical activity between conditions (time window: -1500 to 500 ms, frequency range: 1 – 60 Hz, in steps of 1 Hz, central frequency: 1 Hz, time resolution [full width at half maximum, FWHM]: 2 s). Additionally, we also applied Morlet wavelets to single trial source time series in contralateral SI. We averaged the spectral power for each participant across trials, then normalized the power relative to an averaged baseline of -1300 to -1000 ms, which was determined by taking the edge effect into account. Then, we tested the difference between conditions at the group level. For analyses of the time-frequency domain, we used a non-parametric permutation approach for -1000 to 300 ms (391 samples) and 5 – 60 Hz frequency bands (56 samples) (Monte-Carlo approach, 5000 randomizations) (Maris & Oostenveld, 2007) separately for each ROI to identify significant time and frequency windows using FDR over the dimensions of time and frequency.

Next, we aimed to further investigate the potential relationship between perception and spectral power. The ROI, time window and frequency bands were determined

by the level of significance in the above-mentioned pre-stimulus time-frequency analysis at the group level, resulting in contralateral SI, for -500 to 0 ms and 10- to 15-Hz frequency bands (Figure 4a).

For each trial, we averaged spectral power in 10- to 15-Hz frequency bands for -500 to 0 ms in contralateral SI. We modelled the relationship between the single trial 10- to 15-Hz spectral power and behavioural response using a generalized linear mixed-effects model (GLMM). GLMM is a statistical analysis model that is an extension of the generalized linear model in statistics, which allows for nesting of trial-wise data within each participant and can take into account the variance among participants as a random effect. GLMM was performed using R 4.0.1 (R Core Team, 2020). We used the `glmer` function of the `lme4` package for model fitting (Bates et al., 2015), `lmerTest` package for calculating P values (Kuznetsova et al., 2017) and `Anova` function of the `car` package for Wald tests of the effects (Fox & Weisberg, 2019). The model was specified by the following syntax in R:

```
Perceive ~ Power + (Power | Participant).
```

This syntax indicates that the response variable on the left side of the \sim operator is modelled as a function of the terms on the right side of the \sim operator. Terms outside the brackets specify the fixed effects, whereas terms inside the brackets specify random effects. Thus, the fixed effect was a single trial with 10- to 15-Hz spectral power. Participant was specified as a random effect. We coded 'Perceive' of each trial as 1 if the participant responded to the NT stimulus and 0 if they did not respond.

3 | RESULTS

3.1 | Behaviour

Across all participants, the mean reaction time and hit rate (successfully detected NT) were 0.61 ± 0.12 s (\pm SD) and $41.9 \pm 7.7\%$ (\pm SD), respectively. The mean false alarm rate was $0.2 \pm 0.5\%$. This indicates that participants responded only when they actually perceived the stimuli. This rough balance between hit and miss is in line with previous studies (Hirvonen et al., 2018; Leske et al., 2015; Sadaghiani et al., 2015).

The statistical analysis showed that the main effect of the preceding stimulus type (perceived, unperceived and omitted stimulus) was significant ($F(2,36) = 42.692$, $P < .001$), but the main effects of session (first, second and third) and interaction were not significant ($F(2,36) = 1.432$, $P = .252$ and $F(4,72) = 0.551$, $P = .699$, respectively). The ratio of nonperceived stimulus preceding the

perceived trial was the lowest among the three stimulus types (vs. perceived stimulus: $P < .001$, vs. omitted stimulus: $P < .001$). There was no significant difference between the ratio of the perceived and omitted stimulus ($P < .690$). This result indicated that the omission of stimulus did not have a specific effect on NT stimulus perception.

3.2 | Post-stimulus neuronal activity

Figure 1 shows the averaged time series of the cortical activity extracted from source data across participants, following the NT presentation. Although the first component in the miss condition was smaller than that in hit, an early component (M60) at ~ 60 ms can be clearly identified under both conditions (Figure 1a). The cortical activity at 60 ms from the stimulus onset was identified

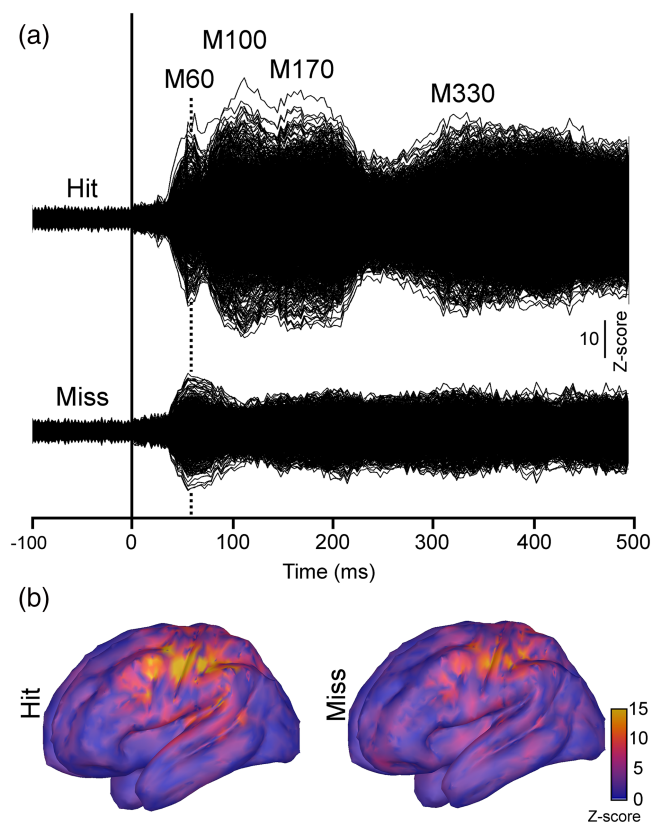


FIGURE 1 Averaged waveforms of time series extracted from source data across participants (a) and cortical activity at 60 ms from the stimulus onset (b). (a) The strength of cortical activity extracted from reconstructed magnetoencephalography (MEG) source data following the near-threshold (NT) stimuli for the hit and miss condition (upper and lower, respectively). The vertical line indicates the onset of somatosensory stimulus. (b) The cortical activity projected on the cortical surface at 60 ms from the stimulus onset in hit and miss

around the pre- and postcentral sulcus over the cortical map (Figure 1b). In the hit condition, three subsequent components (M100, M170 and M320) following M60 were also identified. These components were observed at similar latencies compared with previous reports (Hirvonen et al., 2018; Jones et al., 2007; Palva et al., 2005). On the contrary, in the miss condition, except for M60, no subsequent clear components were identified. Figure 2a shows the averaged time-series waveform and variability across participants in SI and SII for each condition. The parametric test against the baseline in SI revealed that the significant first component started at ~ 40 ms and peaked at ~ 60 ms in both hit and miss conditions (Figure 2a). For SII, significant components started later following SI and peaked at ~ 110 ms in the hit condition, but there was no clear peak in miss (Figure 2a lower). Figure 2b shows the averaged waveform and variability across participants of the subtraction between conditions. For SI, the significant difference in cortical activity between hit and miss appeared after ~ 400 ms but not in the early stage following stimulus onset. On the other hand, in SII, the difference in the strength of cortical activity between conditions was identified after ~ 80 ms and occurred earlier than that in SI.

In spatial dynamic analysis, statistical analysis revealed no significant difference in neural activity in the time window (from 40 to 70 ms) around the M60 component between conditions. On the other hand, several cortical areas showed significantly stronger activity for consciously perceived trials after the M60 component. In the time window (from 70 to 140 ms) around M100, neural activity with a significant difference was observed in the contralateral SII, superior/middle temporal gyrus, postcentral sulcus, orbitofrontal cortex, frontal pole, parieto-occipital sulcus and bilateral ACC ($P < .05$ corrected with FDR) (Figure 3: upper left). In the time window (from 140 to 230 ms) around M170, the bilateral SII, superior/middle temporal gyrus, ACC, orbitofrontal cortex and left inferior frontal cortex were more enhanced in the hit compared with miss condition ($P < .05$ corrected with FDR) (Figure 3: upper right). Similarly, the right inferior parietal, calcarine, bilateral inferior temporal gyrus and parahippocampal were more enhanced in hit in the time window (from 280 to 390 ms) around M320 ($P < .05$ corrected with FDR) (Figure 3: lower).

3.3 | Pre-stimulus power effects

Regarding the cortical area showing a significant difference in the above-mentioned source level analysis, we

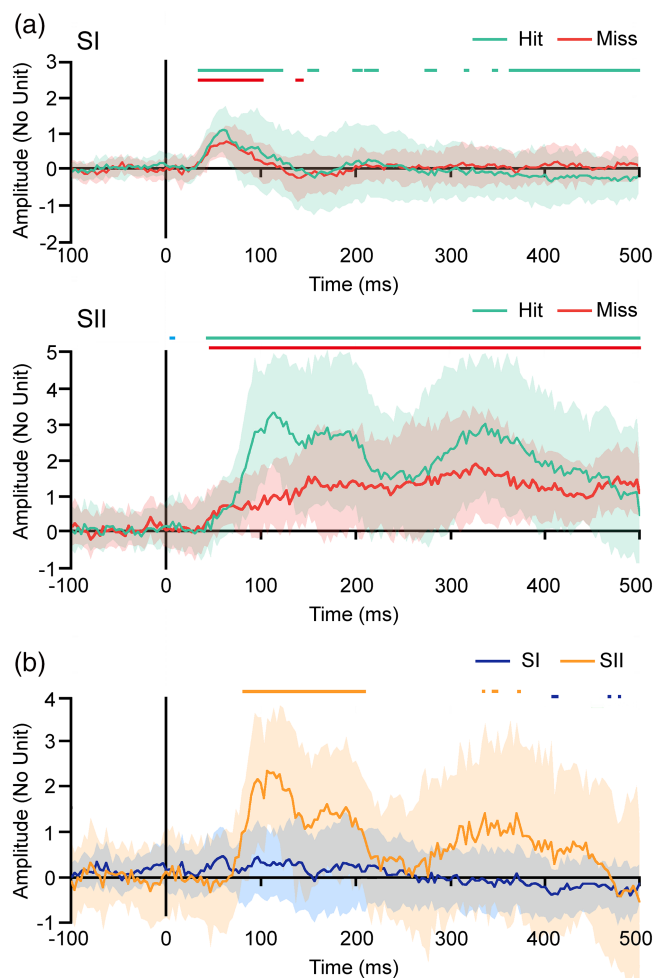


FIGURE 2 Central tendency and variability of time series in hit and miss conditions (a) and of subtraction between conditions (b). (a) The averaged time series of reconstructed magnetoencephalography (MEG) source data extracted from somatosensory area (SI, upper) and secondary somatosensory area (SII, lower). The solid line and coloured shadow indicate the averaged waveform and standard deviation across participants, respectively. The horizontal lines on the upper side indicate the significant components against the baseline (-100 to 0 from stimulus onset) ($P < .05$ with false discovery rate [FDR] correction). (b) The subtracted waveforms between hit and miss conditions, calculated within the participants and averaged across participants. The solid line and coloured shadow indicate averaged waveform and standard deviation across participants, respectively. The horizontal lines on the upper side indicate the time window with significant differences between hit and miss conditions ($P < .05$ with FDR correction)

created a time-frequency map and compared the conditions. Spectral power analysis revealed a significant time window and frequency band in the pre-stimulus period. Only contralateral SI showed a significant difference between conditions on statistical multiple comparison

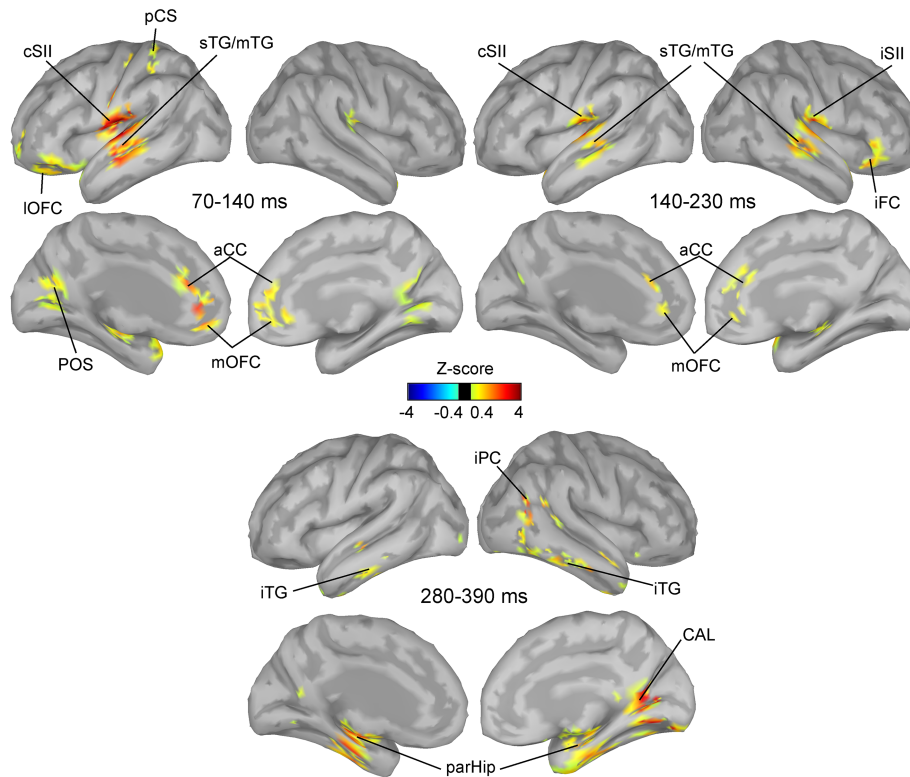


FIGURE 3 Cortical areas with significant differences between hit and miss condition. The cortical areas whose strength of cortical activity was significantly different between hit and miss at each time-window corresponding to M100 (upper left), M170 (upper right) and M330 (lower) in Figure 1 ($P < .05$ with false discovery rate [FDR] correction). The warm colour indicates the stronger cortical activity for perceivable compared with unperceivable stimuli. Acronyms for the brain areas are cSII = contralateral secondary somatosensory area, pCS = postcentral sulcus, sTG/mTG = superior/middle temporal gyrus, IOFC = lateral orbitofrontal cortex, mOFC = medial orbitofrontal cortex, ACC = anterior cingulate cortex, POS = parieto-occipital sulcus, iFC = inferior frontal cortex, iTG = inferior temporal gyrus, iPC = inferior parietal cortex, CAL = calcarine sulcus, parHip = parahippocampus

(Figure 4a), and no other cortical area showed a significant difference in spectral power in the pre-stimulus period. The spectral power within 10–15 Hz for -500 to 0 ms in contralateral SI was significantly decreased in the hit compared with miss condition, which showed that decreased power in contralateral SI preceded consciously perceived NT stimuli (Figure 4a). The frequency band and time window showing a significant difference in time-frequency analysis was focused on in subsequent analysis.

3.4 | Relationship between pre-stimulus alpha power and performance

To examine the relationship between pre-stimulus alpha power in contralateral SI and performance, we fitted the GLMM. For contralateral SI, alpha power was a significant predictor of performance. The estimated coefficient of alpha power was -0.72 (± 0.20 [SE], $\chi^2 = 12.35$, $P = .00044$). This analysis revealed that, in all trials, an

increase in alpha power indicated a lower probability of reporting perceive (Figure 4b).

4 | DISCUSSION

We investigated the cortical areas with a difference in cortical activity between hit and miss conditions and, then, related to cortical areas with significant differences, clarified whether there was a significant difference in the pre-stimulus alpha power. By analysing the source reconstructed data, we were able to examine the brain regions showing enhanced cortical activity following the NT stimulus in the whole brain. The present study identified several cortical regions whose evoked responses predict subsequent conscious access to NT somatosensory stimuli. These cortical regions were the unimodal association areas, that is, higher-order somatosensory-related regions, and the multimodal association areas, but contralateral SI, which is the primary area in somatosensory information processing, showed no difference in cortical

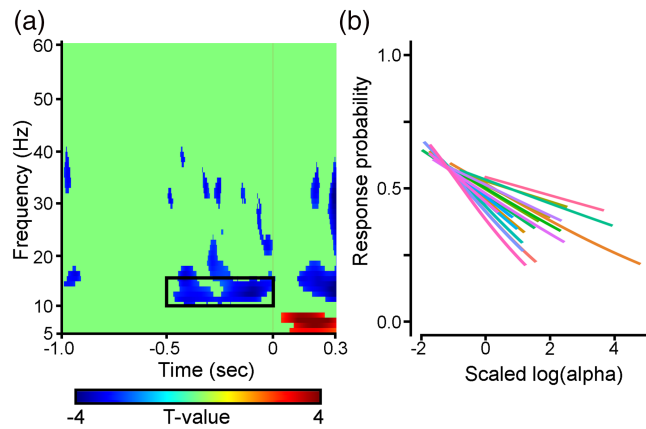


FIGURE 4 Pre-stimulus oscillation power at source level and correlation with perceptual performance in contralateral somatosensory area (SI). (a) The significant spectral power in time-frequency representations of the contralateral SI on comparing hit with miss trials ($P < .05$ with false discovery rate [FDR] correction). The black rectangle shows the time-frequency windows used for subsequent power-perceptual performance analysis (b) (alpha: 10–15 Hz, –500 to 0 ms). The time 0 ms indicates the onset of stimulation. (b) Colour lines indicate the estimated relationship between perceptual performance and alpha power in each participant

activity during the early processing period between hit and miss conditions. On the other hand, for the spectral power in the pre-stimulus period, only the neuronal oscillation in contralateral SI showed a significant difference in the alpha frequency band, but there was no difference in other regions. Together, these findings suggest that the neural activity after processing in SI is an important component for the conscious perception of an NT somatosensory stimulus. Further, the pre-stimulus alpha activity in SI may contribute to the cortical activity in SI after the early stage of NT stimulus processing.

4.1 | Contribution of post-stimulus cortical activity to conscious perception

We observed the early component M60 at contralateral SI at ~60 ms from the stimulus onset in consciously perceived and unperceived conditions. While previous studies using EEG and MEG (Auzztulewicz et al., 2012; Linkenkaer-Hansen et al., 2004; Nierhaus et al., 2015; Palva et al., 2005; Zhang & Ding, 2010) suggested the existence of at least one early component at ~60 ms following NT stimuli, this component has not yet been demonstrated in a MEG study using source reconstructed data. This is the first study demonstrating the early component following both perceived and unperceived NT somatosensory stimuli. The strength of cortical activity

during the time window corresponding to this M60 component was not different between hit and miss, supporting the previous scalp-sensor-level EEG and MEG studies (Auzztulewicz et al., 2012; Zhang & Ding, 2010). Further, a single cell recording study in monkeys showing no significant difference in the activity of SI neurons between perceived and unperceived trials is also in line with our finding (de Lafuente & Romo, 2005). The early incoming wave of sensory-evoked activity (P1 and N1) in unperceived trials was recorded in the visual domain, which supports our results, suggesting that early brain activities may not be primary correlates of conscious perception (Sergent et al., 2005; Shahidi et al., 2019). However, contrary to our results, a previous study using MEG reconstructed source data showed that the early component corresponding to M60 in our study predicted subsequent conscious perception (Hirvonen & Palva, 2016). This inconsistency in involvement of initial components may be explained by the characteristics of the M60 component being affected by the stimulus parameters (Wikström et al., 1996).

Regarding the neurophysiological interpretation of M60, a computational SI modelling study demonstrated that the first SI response predicting detection was observed at ~70 ms, corresponding to M60 in our study, and was induced by exogenous excitatory input to the supragranular layer of SI of which candidate sources were feedback from SII or other higher-order areas (Jones et al., 2007). Together with previous studies, our findings indicate the possibility that although earlier components in SII are invisible due to the low signal to noise ratio, a series of cortical processing until excitatory inputs from SII or other regions reach SI is independent of conscious perception of NT somatosensory stimuli. The M60 component is a necessary condition for subsequent conscious perception (Dehaene & Changeux, 2011; Nierhaus et al., 2015). Our other results showing no clear cortical activity for unperceived stimuli in SI after M60 provide partial support for this together with a previous study showing that unperceived NT processing is terminated at an early stage in SI (Nierhaus et al., 2015). In addition to that, significant differences in cortical activity between hit and miss were observed after ~400 ms in SI and after ~80 ms in SII in our recordings, suggesting that the divergence of the processing of NT leading to conscious perception occurs after at least 80 ms after. Because the latency of our findings was later than that of the early incoming wave of sensory-evoked activity, these findings support late entry rather than early entry of the NT stimulus to consciousness, which is in line with that in the visual domain (Forget et al., 2010; Vul & MacLeod, 2006). Intriguingly, this divergence started from SII but not SI. The timing and area of divergence

are consistent with a previous study applying dynamic causal modelling to examine the recurrent neural processing within somatosensory-related areas (Auzstulewicz et al., 2012), which showed an early contralateral SI component peaking independent of stimulus detection at ~60 ms and a divergent activity pattern in contralateral SII followed by the later divergence in contralateral SI.

Regarding brain regions predicting conscious perception other than SI, significantly enhanced cortical activity was observed in SII, postcentral sulcus and parahippocampal regions, which belong to areas of somatosensory hierarchical processing (Felleman & Van Essen, 1991; Hirvonen & Palva, 2016). Depending on the latency from stimulus onset, the difference of cortical activity in somatosensory-related areas widely spread from the contra-lateral (left) towards bilateral hemisphere and from somatosensory-related regions except for SI towards multimodality regions, following a manner of somatosensory hierarchical processing (Felleman & Van Essen, 1991). This result is in line with the findings in the visual domain in which the late wave of activation spread through the distributed network of cortical association areas in perceived trials (Sergent et al., 2005). In addition to somatosensory hierarchical regions, enhanced cortical activity was also observed in medial prefrontal and posteromedial regions, which belong to default mode network (DMN) (Douw et al., 2016; Gonzalez-Castillo & Bandettini, 2018; Sadaghiani et al., 2015). A previous MEG study revealed that neuronal oscillations in regions belonging to DMN predict conscious somatosensory perception (Hirvonen & Palva, 2016). Furthermore, previous functional MRI (fMRI) studies observed that the BOLD signal in DMN regions is positively correlated with conscious visual and auditory perception (Chica et al., 2016; Sadaghiani et al., 2009). Intriguingly, several recent studies demonstrated that task-concurrent dynamic functional networks, for example, DMN, are correlated with behavioural performance in several types of task (Braun et al., 2015; Douw et al., 2016; Elton & Gao, 2015; Gonzalez-Castillo & Bandettini, 2018). Therefore, modulation of neuronal activity in DMN might effect on in conscious NT somatosensory perception.

We also observed stronger cortical activity in the orbitofrontal and inferior frontal cortex for consciously perceived stimuli. Previous source-reconstructed MEG studies using several sensory modalities indicated that superior, medial and inferior frontal cortical areas contribute to conscious perception of sensory stimuli (Brancucci et al., 2011; Hirvonen & Palva, 2016; Salti et al., 2015). Our findings are in line with these previous studies. The prefrontal areas showed stronger cortical activity at an early stage of somatosensory processing

when the contralateral SII showed a significant difference between hit and miss conditions. Together with previous studies, we demonstrated that neuronal activity in prefrontal areas may play important roles in somatosensory awareness (Dehaene & Changeux, 2011).

4.2 | Contribution of pre-stimulus neuronal oscillation

In the pre-stimulus period, we observed significantly decreased alpha power in contralateral SI preceding conscious perception. Pre-stimulus alpha power modulates baseline excitability and alters response bias, which results in preferring to respond 'yes,' but it does not alter sensitivity (Iemi et al., 2017). A similar effect was reported across multiple sensory modalities (Helfrich et al., 2014; Iemi et al., 2017; Strauß et al., 2015). Further, in the somatosensory domain, this is causally confirmed by modulation of alpha power by transcranial alternating current stimulation (Craddock et al., 2019). In this study, we observed a negative linear trend between alpha power in contralateral SI and the performance, supporting the baseline model (Iemi et al., 2017). However, we observed the early component at ~60 ms in contralateral SI when consciously perceived and in unperceived trials, and no difference in the strength of cortical activity until <400 ms from the stimulus onset between perceived and unperceived trials. Such a discrepancy may be explained by two hypotheses. Following the granular output evoked by thalamic input, for unperceived trials, alpha cortical oscillation weakens the exogenous excitatory input to the supragranular layer of SI from SII or other higher order cortex (Jones et al., 2007) and disturbs the trigger of subsequent recurrent neural processing from SI to SII (Auzstulewicz et al., 2012), which resulted in the observation of M60 and no other components in unperceived trials. This mechanism may also explain the decreased and delayed M60 observed in some previous studies (Nierhaus et al., 2015; Palva et al., 2005). Alternatively, after M60, alpha oscillation inhibits the layer II/III pyramidal cells and also subsequent recurrent neural processing from SI to SII (Halgren et al., 2019). This hypothesis is in line with previous studies reporting that supragranular origin alpha oscillation plays a role in neural inhibition (Haegens, Nacher, et al., 2011; Larkum, 2013).

While we observed the fluctuation of alpha power in contralateral SI, other regions showed no significant difference in pre-stimulus oscillation, despite the cortical activity in these regions being stronger for the consciously perceived trials. Our results indicate that, only in contralateral SI, the fluctuation of cortical activity can be

explained by the pre-stimulus alpha power fluctuation, suggesting that the pre-stimulus oscillation pattern only in SI may be one of the constituents of the subsequent conscious perception of NT somatosensory stimuli (Baumgarten et al., 2016; Jones et al., 2010; Schubert et al., 2009; Wittenberg et al., 2018). Therefore, the fluctuation of cortical activity in somatosensory hierarchical cortical areas except SI might not be due to fluctuation of the pre-stimulus alpha power but simply express somatosensory information processing following cortical activity in SI. Here, it should be noted that this study demonstrated an indirect link between the pre-stimulus alpha fluctuation and post-stimulus cortical activity in contralateral SI. We cannot examine the direct relationship between them using our experimental design. Further study is needed to test the direct relationship between the pre-stimulus alpha power and post-stimulus cortical activity.

On the other hand, it should be mentioned that fluctuation of the pre-stimulus alpha power might reflect the allocation of attentional resources (Haegens et al., 2012; Haegens, N acher, et al., 2011; van Ede et al., 2014). Previous studies reported that fluctuation of the alpha power modulates somatosensory perception and that this fluctuation is under top-down control (Haegens, N acher, et al., 2011; Linkenkaer-Hansen et al., 2004; Zhang & Ding, 2010). This is supported by previous studies suggesting that alpha power in somatosensory regions is modulated by frontal regions (Haegens et al., 2012; Zhang & Ding, 2010). Taking these findings into account, fluctuation of the pre-stimulus alpha power in this study may be affected by an attention difference between perceived and unperceived stimuli, regardless of whether participants were conscious of it during MEG recording.

Finally, it should be noted that the statistical interpretation of the results in the time-frequency domain in this study must take into account the dangers of circular analysis (Kriegeskorte et al., 2010). The ROI selection based on the time-domain conditional contrast in the analysis of the time-frequency domain is circular and can introduce a bias, which increases the likelihood of a type I error, even though two analyses in pre- and post-stimulus phases showed a different analysis time window and analysis domain.

5 | CONCLUSION AND LIMITATIONS

We studied the pre-stimulus oscillation pattern and post-stimulus cortical activity following NT somatosensory stimuli. With the use of the reconstructed MEG source

data, we firstly identified the early component following both perceived and unperceived weak somatosensory stimuli in SI. Additionally, we observed that the somatosensory hierarchical processing areas excluding SI, prefrontal areas and cortical areas belonging to DMN showed stronger cortical activity for consciously perceived trials in the post-stimulus period. These findings suggest that the bottom-up stream of somatosensory information flow following SI and also top-down modulation play important roles in the conscious perception of NT somatosensory stimuli. Further, we revealed the fluctuation of pre-stimulus oscillation only in SI and not in other regions. These findings provide evidence that the effect of the pre-stimulus oscillation fluctuation on SI is one of the constituents of subsequent somatosensory awareness. Furthermore, the pre-stimulus alpha fluctuation on SI may have an effect on the cortical activity in SI after the early stage of NT stimulus processing.

There are some limitations regarding interpreting the results of this study. First, the NT stimulus detection paradigm in this study is different from that in previous studies regarding the presence of cues indicating the onset of stimulus presentation. This difference might indicate the difficulty of the detection task and has led to a decrease in the detection rate compared with those in previous studies. Furthermore, by changing the task paradigm, we cannot comment on the effect of psychological functions (e.g., attention) on our results (Weisz et al., 2014). However, by analysing the number of hit and miss trials in equal numbers, we were able to reproduce the results of previous studies in time-frequency and reconstructed source analyses. Next, because the interval between the button press (average: 600 ms) and the start of the baseline of the next trial (-1.3 s) was ~ 600 ms in the shortest interstimulus interval (2.5 s), there is a possibility that the late potentials of the response to consciously perceived stimuli may have affected the baseline of the next trial. Finally, the difference in brain parcellation is likely to influence the results (Gonzalez-Castillo & Bandettini, 2018). This difference may make comparison across studies challenging. Unfortunately, there is no consensus regarding the most optimized brain parcellation. Additional research on how to apply appropriate brain parcellation to optimally estimate the conscious perception of NT stimuli is needed.

ACKNOWLEDGEMENT

This work was supported by Japan Society for the Promotion of Science KAKENHI Grant Number 17K01499 and 20K11154.

CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

AUTHOR CONTRIBUTIONS

J.U., A.H., G.I., M.C. and M.H. contributed to the study conception and design. Data recording and analysis were performed by J.U. and M.H. Statistical evaluation were performed by J.U. and Y.M. The draft of the manuscript was written by J.U. and M.H. and corrected and commented on by all authors. All authors contributed towards projection administration and read and approved the final manuscript.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ejn.15388>.

DATA AVAILABILITY STATEMENT

Due to ethical considerations, the provision of data in this study to other facilities is not approved by ethical committee and will not be shared.

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REFERENCES

- Ai, L., & Ro, T. (2014). The phase of prestimulus alpha oscillations affects tactile perception. *Journal of Neurophysiology*, *111*(6), 1300–1307. <https://doi.org/10.1152/jn.00125.2013>
- Auksztulewicz, R., Spitzer, B., & Blankenburg, F. (2012). Recurrent neural processing and somatosensory awareness. *Journal of Neuroscience*, *32*(3), 799–805. <https://doi.org/10.1523/JNEUROSCI.3974-11.2012>
- Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1). <https://doi.org/10.18637/jss.v067.i01>
- Baumgarten, T. J., Schnitzler, A., & Lange, J. (2016). Prestimulus alpha power influences tactile temporal perceptual discrimination and confidence in decisions. *Cerebral Cortex*, *26*(3), 891–903. <https://doi.org/10.1093/cercor/bhu247>
- Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society, Series B*, *57*(1), 289–300.
- Boly, M., Balteau, E., Schnakers, C., Degueldre, C., Moonen, G., Luxen, A., Phillips, C., & Peigneux, P. (2007). Baseline brain activity fluctuations predict somatosensory perception in humans. *Proceedings of the National Academy of Sciences*, *104*(Table 1), 12187–12192. <https://doi.org/10.1073/pnas.0611404104>
- Brancucci, A., Franciotti, R., D'Anselmo, A., della Penna, S., & Tommasi, L. (2011). The sound of consciousness: Neural underpinnings of auditory perception. *Journal of Neuroscience*, *31*(46), 16611–16618. <https://doi.org/10.1523/JNEUROSCI.3949-11.2011>
- Braun, U., Schäfer, A., Walter, H., Erk, S., Romanczuk-Seiferth, N., Haddad, L., Schweiger, J. I., Grimm, O., Heinz, A., Tost, H., Meyer-Lindenberg, A., & Bassett, D. S. (2015). Dynamic reconfiguration of frontal brain networks during executive cognition in humans. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(37), 11678–11683. <https://doi.org/10.1073/pnas.1422487112>
- Chica, A. B., Bayle, D. J., Botta, F., Bartolomeo, P., & Paz-Alonso, P. M. (2016). Interactions between phasic alerting and consciousness in the fronto-striatal network. *Scientific Reports*, *6*(February), 1–13. <https://doi.org/10.1038/srep31868>
- Craddock, M., Klepousniotou, E., El-Deredy, W., Poliakoff, E., & Lloyd, D. (2019). Transcranial alternating current stimulation at 10 Hz modulates response bias in the somatic signal detection task. *International Journal of Psychophysiology*, *135*-(June 2018), 106–112. <https://doi.org/10.1016/j.ijpsycho.2018.12.001>
- de Lafuente, V., & Romo, R. (2005). Neuronal correlates of subjective sensory experience. *Nature Neuroscience*, *8*(12), 1698–1703. <https://doi.org/10.1038/nn1587>
- Dehaene, S., & Changeux, J.-P. (2011). Experimental and theoretical approaches to conscious processing. *Neuron*, *70*(2), 200–227. <https://doi.org/10.1016/j.neuron.2011.03.018>
- Destrieux, C., Fischl, B., Dale, A., & Halgren, E. (2010). Automatic parcellation of human cortical gyri and sulci using standard anatomical nomenclature. *NeuroImage*, *53*(1), 1–15. <https://doi.org/10.1016/j.neuroimage.2010.06.010>
- Douw, L., Wakeman, D. G., Tanaka, N., Liu, H., & Stufflebeam, S. M. (2016). State-dependent variability of dynamic functional connectivity between frontoparietal and default networks relates to cognitive flexibility. *Neuroscience*, *339*, 12–21. <https://doi.org/10.1016/j.neuroscience.2016.09.034>
- Elton, A., & Gao, W. (2015). Task-related modulation of functional connectivity variability and its behavioral correlations. *Human Brain Mapping*, *36*(8), 3260–3272. <https://doi.org/10.1002/hbm.22847>
- Felleman, D. J., & van Essen, D. C. (1991). Distributed hierarchical processing in the primate cerebral cortex. *Cerebral Cortex*, *1*(1), 1–47. <https://doi.org/10.1093/cercor/1.1.1>
- Forget, J., Buiatti, M., & Dehaene, S. (2010). Temporal integration in visual word recognition. *Journal of Cognitive Neuroscience*, *22*(5), 1054–1068. <https://doi.org/10.1162/jocn.2009.21300>
- Fox, J., & Weisberg, S. (2019). *An R Companion to Applied Regression (third edit)*. Sage. <https://socialsciences.mcmaster.ca/jfox/Books/Companion/>
- Frey, J. N., Ruhnau, P., Leske, S., Siegel, M., Braun, C., & Weisz, N. (2016). The tactile window to consciousness is characterized by frequency-specific integration and segregation of the primary somatosensory cortex. *Scientific Reports*, *6*(November 2015), 1–8. <https://doi.org/10.1038/srep20805>
- Gonzalez-Castillo, J., & Bandettini, P. A. (2018). Task-based dynamic functional connectivity: Recent findings and open questions. *NeuroImage*, *180*(May 2017), 526–533. <https://doi.org/10.1016/j.neuroimage.2017.08.006>
- Haegens, S., Luther, L., & Jensen, O. (2012). Somatosensory anticipatory alpha activity increases to suppress distracting input. *Journal of Cognitive Neuroscience*, *24*(3), 677–685. https://doi.org/10.1162/jocn_a_00164
- Haegens, S., Nacher, V., Luna, R., Romo, R., & Jensen, O. (2011). Oscillations in the monkey sensorimotor network influence discrimination performance by rhythmical inhibition of neuronal spiking. *Proceedings of the National Academy of*

- Sciences*, 108(48), 19377–19382. <https://doi.org/10.1073/pnas.1117190108>
- Haegens, S., Nácher, V., Luna, R., Romo, R., & Jensen, O. (2011). α -Oscillations in the monkey sensorimotor network influence discrimination performance by rhythmical inhibition of neuronal spiking. *Proceedings of the National Academy of Sciences of the United States of America*, 108(48), 19377–19382. <https://doi.org/10.1073/pnas.1117190108>
- Halgren, M., Ulbert, I., Bastuji, H., Fabó, D., Eross, L., Rey, M., Devinsky, O., Doyle, W. K., Mak-McCully, R., Halgren, E., Wittner, L., Chauvel, P., Heit, G., Eskandar, E., Mandell, A., & Cash, S. S. (2019). The generation and propagation of the human alpha rhythm. *Proceedings of the National Academy of Sciences of the United States of America*, 116(47), 23772–23782. <https://doi.org/10.1073/pnas.1913092116>
- Hämäläinen, M. S., & Ilmoniemi, R. J. (1994). Interpreting magnetic fields of the brain: Minimum norm estimates. *Medical & Biological Engineering & Computing*, 32(1), 35–42. <https://doi.org/10.1007/BF02512476>
- Hanslmayr, S., Aslan, A., Staudigl, T., Klimesch, W., Herrmann, C. S., & Bäuml, K. H. (2007). Prestimulus oscillations predict visual perception performance between and within subjects. *NeuroImage*, 37(4), 1465–1473. <https://doi.org/10.1016/j.neuroimage.2007.07.011>
- Helfrich, R. F., Schneider, T. R., Rach, S., Trautmann-Lengsfeld, S. A., Engel, A. K., & Herrmann, C. S. (2014). Entrainment of brain oscillations by transcranial alternating current stimulation. *Current Biology*, 24(3), 333–339. <https://doi.org/10.1016/j.cub.2013.12.041>
- Hirvonen, J., Monto, S., Wang, S. H., Palva, J. M., & Palva, S. (2018). Dynamic large-scale network synchronization from perception to action. *Network Neuroscience*, 2(4), 442–463. https://doi.org/10.1162/netn_a_00039
- Hirvonen, J., & Palva, S. (2016). Cortical localization of phase and amplitude dynamics predicting access to somatosensory awareness. *Human Brain Mapping*, 37(1), 311–326. <https://doi.org/10.1002/hbm.23033>
- Iemi, L., Chaumon, M., Crouzet, S. M., & Busch, N. A. (2017). Spontaneous neural oscillations bias perception by modulating baseline excitability. *Journal of Neuroscience*, 37(4), 807–819. <https://doi.org/10.1523/JNEUROSCI.1432-16.2016>
- Jensen, O., & Mazaheri, A. (2010). Shaping functional architecture by oscillatory alpha activity: Gating by inhibition. *Frontiers in Human Neuroscience*, 4(November), 186. <https://doi.org/10.3389/fnhum.2010.00186>
- Jones, S. R., Kerr, C. E., Wan, Q., Pritchett, D. L., Hamalainen, M., & Moore, C. I. (2010). Cued spatial attention drives functionally relevant modulation of the mu rhythm in primary somatosensory cortex. *Journal of Neuroscience*, 30(41), 13760–13765. <https://doi.org/10.1523/JNEUROSCI.2969-10.2010>
- Jones, S. R., Pritchett, D. L., Stufflebeam, S. M., Hämäläinen, M., & Moore, C. I. (2007). Neural correlates of tactile detection: A combined magnetoencephalography and biophysically based computational modeling study. *Journal of Neuroscience*, 27(40), 10751–10764. <https://doi.org/10.1523/JNEUROSCI.0482-07.2007>
- Kakigi, R., Hoshiyama, M., Shimojo, M., Naka, D., Yamasaki, H., Watanabe, S., Xiang, J., Maeda, K., Lam, K., Itomi, K., & Nakamura, A. (2000). The somatosensory evoked magnetic fields. *Progress in Neurobiology*, 61(5), 495–523. [https://doi.org/10.1016/S0301-0082\(99\)00063-5](https://doi.org/10.1016/S0301-0082(99)00063-5)
- Klimesch, W., Sauseng, P., & Hanslmayr, S. (2007). EEG alpha oscillations: The inhibition-timing hypothesis. *Brain Research Reviews*, 53(1), 63–88. <https://doi.org/10.1016/j.brainresrev.2006.06.003>
- Kriegeskorte, N., Simmons, W. K., Bellgowan, P. S. F., & Baker, C. I. (2010). Circular analysis in systems neuroscience: The dangers of double dipping. *Nature Neuroscience*, 12(5), 535–540. <https://doi.org/10.1038/nn.2303>
- Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software*, 82(13). <https://doi.org/10.18637/jss.v082.i13>
- Lange, J., Halacz, J., van Dijk, H., Kahlbrock, N., & Schnitzler, A. (2012). Fluctuations of prestimulus oscillatory power predict subjective perception of tactile simultaneity. *Cerebral Cortex*, 22(11), 2564–2574. <https://doi.org/10.1093/cercor/bhr329>
- Larkum, M. (2013). A cellular mechanism for cortical associations: An organizing principle for the cerebral cortex. *Trends in Neurosciences*, 36(3), 141–151. <https://doi.org/10.1016/j.tins.2012.11.006>
- Leske, S., Ruhnau, P., Frey, J., Lithari, C., Müller, N., Hartmann, T., & Weisz, N. (2015). Prestimulus network integration of auditory cortex predisposes near-threshold perception independently of local excitability. *Cerebral Cortex*, 25(12), 4898–4907. <https://doi.org/10.1093/cercor/bhv212>
- Linkenkaer-Hansen, K., Nikulin, V. V., Palva, S., Ilmoniemi, R. J., & Palva, J. M. (2004). Prestimulus oscillations enhance psychophysical performance in humans. *Journal of Neuroscience*, 24(45), 10186–10190. <https://doi.org/10.1523/JNEUROSCI.2584-04.2004>
- Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG- and MEG-data. *Journal of Neuroscience Methods*, 164(1), 177–190. <https://doi.org/10.1016/j.jneumeth.2007.03.024>
- Morillon, B., & Baillet, S. (2017). Motor origin of temporal predictions in auditory attention. *Proceedings of the National Academy of Sciences of the United States of America*, 114(42), E8913–E8921. <https://doi.org/10.1073/pnas.1705373114>
- Nierhaus, T., Forschack, N., Piper, S. K., Holtze, S., Krause, T., Taskin, B., Long, X., Stelzer, J., Margulies, D. S., Steinbrink, J., & Villringer, A. (2015). Imperceptible somatosensory stimulation alters sensorimotor background rhythm and connectivity. *Journal of Neuroscience*, 35(15), 5917–5925. <https://doi.org/10.1523/JNEUROSCI.3806-14.2015>
- Nolte, G., & Curio, G. (1999). The effect of artifact rejection by signal-space projection on source localization accuracy in MEG measurements. *IEEE Transactions on Bio-Medical Engineering*, 46(4), 400–408. <http://www.ncbi.nlm.nih.gov/pubmed/10217878>
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, 9(1), 97–113. [https://doi.org/10.1016/0028-3932\(71\)90067-4](https://doi.org/10.1016/0028-3932(71)90067-4)
- Palva, S., Linkenkaer-Hansen, K., Näätänen, R., & Palva, J. M. (2005). Early neural correlates of conscious somatosensory perception. *Journal of Neuroscience*, 25(21), 5248–5258. <https://doi.org/10.1523/JNEUROSCI.0141-05.2005>

- R Core Team (2020). *R: A language and environment for statistical computing*. <https://www.r-project.org/>
- Sadaghiani, S., Hesselmann, G., & Kleinschmidt, A. (2009). Distributed and antagonistic contributions of ongoing activity fluctuations to auditory stimulus detection. *Journal of Neuroscience*, 29(42), 13410–13417. <https://doi.org/10.1523/jneurosci.2592-09.2009>
- Sadaghiani, S., Poline, J.-B., Kleinschmidt, A., & D'Esposito, M. (2015). Ongoing dynamics in large-scale functional connectivity predict perception. *Proceedings of the National Academy of Sciences*, 112(27), 8463–8468. <https://doi.org/10.1073/pnas.1420687112>
- Salti, M., Monto, S., Charles, L., King, J. R., Parkkonen, L., & Dehaene, S. (2015). Distinct cortical codes and temporal dynamics for conscious and unconscious percepts. *eLife*, 4 (MAY), 1–52. <https://doi.org/10.7554/eLife.05652>
- Schubert, R., Haufe, S., Blankenburg, F., Villringer, A., & Curio, G. (2009). Now you'll feel it, now you won't: EEG rhythms predict the effectiveness of perceptual masking. *Journal of Cognitive Neuroscience*, 21(12), 2407–2419. <https://doi.org/10.1162/jocn.2008.21174>
- Sergent, C., Baillet, S., & Dehaene, S. (2005). Timing of the brain events underlying access to consciousness during the attentional blink. *Nature Neuroscience*, 8(10), 1391–1400. <https://doi.org/10.1038/nn1549>
- Shahidi, N., Andrei, A. R., Hu, M., & Dragoi, V. (2019). High-order coordination of cortical spiking activity modulates perceptual accuracy. *Nature Neuroscience*, 22(7), 1148–1158. <https://doi.org/10.1038/s41593-019-0406-3>
- Strauß, A., Henry, M. J., Scharinger, M., & Obleser, J. (2015). Alpha phase determines successful lexical decision in noise. *Journal of Neuroscience*, 35(7), 3256–3262. <https://doi.org/10.1523/JNEUROSCI.3357-14.2015>
- Tadel, F., Baillet, S., Mosher, J. C., Pantazis, D., & Leahy, R. M. (2011). Brainstorm: A user-friendly application for MEG/EEG analysis. *Computational Intelligence and Neuroscience*, 2011, 1–13. <https://doi.org/10.1155/2011/879716>
- van Ede, F., Szabéni, S., & Maris, E. (2014). Attentional modulations of somatosensory alpha, beta and gamma oscillations dissociate between anticipation and stimulus processing. *NeuroImage*, 97, 134–141. <https://doi.org/10.1016/j.neuroimage.2014.04.047>
- Vul, E., & MacLeod, D. I. A. (2006). Contingent aftereffects distinguish conscious and preconscious color processing. *Nature Neuroscience*, 9(7), 873–874. <https://doi.org/10.1038/nn1723>
- Weisz, N., Wuhle, A., Monittola, G., Demarchi, G., Frey, J., Popov, T., & Braun, C. (2014). Prestimulus oscillatory power and connectivity patterns predispose conscious somatosensory perception. *Proceedings of the National Academy of Sciences*, 111(4), E417–E425. [https://doi.org/10.1016/S0140-6736\(01\)53015-9](https://doi.org/10.1016/S0140-6736(01)53015-9)
- Wikström, H., Huttunen, J., Korvenoja, A., Virtanen, J., Salonen, O., Aronen, H., & Ilmoniemi, R. J. (1996). Effects of interstimulus interval on somatosensory evoked magnetic fields (SEFs): A hypothesis concerning SEF generation at the primary sensorimotor cortex. *Electroencephalography and Clinical Neurophysiology - Evoked Potentials*, 100(6), 479–487. [https://doi.org/10.1016/S0168-5597\(96\)95688-9](https://doi.org/10.1016/S0168-5597(96)95688-9)
- Wittenberg, M. A., Baumgarten, T. J., Schnitzler, A., & Lange, J. (2018). U-shaped relation between prestimulus alpha-band and poststimulus gamma-band power in temporal tactile perception in the human somatosensory cortex. *Journal of Cognitive Neuroscience*, 30(4), 552–564. https://doi.org/10.1162/jocn_a_01219
- Wühle, A., Mertiens, L., Rüter, J., Ostwald, D., & Braun, C. (2010). Cortical processing of near-threshold tactile stimuli: An MEG study. *Psychophysiology*, 47(3), 523–534. <https://doi.org/10.1111/j.1469-8986.2010.00964.x>
- Wühle, A., Preissl, H., & Braun, C. (2011). Cortical processing of near-threshold tactile stimuli in a paired-stimulus paradigm—An MEG study. *European Journal of Neuroscience*, 34(4), 641–651. <https://doi.org/10.1111/j.1460-9568.2011.07770.x>
- Zhang, Y., & Ding, M. (2010). Detection of a weak somatosensory stimulus: Role of the prestimulus mu rhythm and its top-down modulation. *Journal of Cognitive Neuroscience*, 22(2), 307–322. <https://doi.org/10.1162/jocn.2009.21247>

How to cite this article: Uemura, J., Hoshino, A., Igarashi, G., Matsui, Y., Chishima, M., & Hoshiyama, M. (2021). Pre-stimulus alpha oscillation and post-stimulus cortical activity differ in localization between consciously perceived and missed near-threshold somatosensory stimuli. *European Journal of Neuroscience*, 54(4), 5518–5530. <https://doi.org/10.1111/ejn.15388>