NeuroImage 49 (2010) 1777–1785

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

Cortical dynamics of selective attention to somatosensory events

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ARTICLE INFO

Article history:
Received 11 May 2009
Revised 26 August 2009
Accepted 16 September 2009
Available online 23 September 2009

Keywords:
Attention
Somatosensory cortex
Cortical oscillations
Magnetoencephalography
Alpha
Beta
Gamma
Phase-locking
Median nerve stimulation

ABSTRACT

Recent studies have shown evidence of somatosensory deficits in individuals with attentional difficulties yet relatively little is known about the role of attention in the processing of somatosensory input. Neuromagnetic imaging studies have shown that rhythmic oscillations within the human somatosensory cortex are strongly modulated by somatosensory stimulation and may reflect the normal processing of such stimuli. However, few studies have examined how attention influences these cortical oscillations. We examined attentional effects on human somatosensory oscillations during median nerve stimulation by conducting time–frequency analyses of neuromagnetic recordings in healthy adults. We found that selective attention modulated somatosensory oscillations in the alpha, beta, and gamma bands that were both phase-locked and non-phase-locked to the stimulus. In the primary somatosensory cortex (SI), directing the subject's attention toward the somatosensory stimulus resulted in increased gamma band power (30–55 Hz) that was phase-locked to stimulus onset. Directed attention also produced an initial suppression (desynchrony) followed by enhancement (synchrony) of beta band power (13–25 Hz) that was not phase-locked to the stimulus. In the secondary somatosensory cortex (SII), directing attention towards the stimulus increased phase-locked alpha (7–9 Hz) power approximately 30 ms after onset of phase-locked gamma in SI, followed by a non-phase-locked increase in alpha power. We suggest that earlier phase-locked oscillatory power may reflect the relay of input from SI to SII, whereas later non-phase-locked rhythms reflect stimulus-induced oscillations that are modulated by selective attention and may thus reflect enhanced processing of the stimulus underlying the perception of somatosensory events.

Introduction

Attention to a particular object or event while ignoring others (i.e., selective attention) optimizes task performance by ensuring that the underlying neural activities operate efficiently (Fahle, 2009; Hillyard, 1993; Kok et al., 2006; Naatanen and Michie, 1979). Neural efficiency can be indexed by measuring changes in synchronous firing of large cortical assemblies within specific frequency bands. Substantial evidence from studies of auditory and visual selective attention indicates that neural synchrony increases within the gamma band (30–120 Hz) in the modality-relevant primary cortex and also in higher-order regions such as association areas and the frontal lobes (Driver and Frackowiak, 2001; Herrmann and Knight, 2001; Knudsen, 2007). Moreover, recent evidence suggests that changes in the synchrony of lower frequencies such as alpha (8–12 Hz) (Palva and Palva, 2007; Thut et al., 2006; Worden et al., 2000) and beta (13–30 Hz) (Bekisz and Wrobel, 2003; Wrobel, 2000; Wrobel et al., 2007) also accompany increases in attention. The basic premise underlying the effectiveness of neural synchrony is that large groups of neurons are more likely to communicate effectively with their downstream recipients when they are firing in synchrony than when they are asynchronous, due to more efficient summation of their action potentials (Fries et al., 2001; Niebur, 2002; Niebur et al., 2002). Thus, selective attention and the potentiation of neural synchrony optimizes neural communication within and between behaviourally-related regions.

A number of new findings highlight somatosensory processing deficits in individuals with attentional difficulties (Broring et al., 2008; Georgiou-Karistianis et al., 2003; Parush et al., 1997, 2007; Scherder et al., 2008). However, little is known about the effect of selective attention on somatosensory processing in either healthy individuals or clinical populations. Currently two studies of healthy adults have investigated non-painful, attention-related changes to neural synchrony in the human somatosensory cortex. Both suggest that attention directed toward a passive somatosensory event increases gamma synchrony in the somatosensory cortex (Bauer et al., 2006; Ray et al., 2008).

A somatosensory stimulus elicits an early, event-related potential or field in the primary somatosensory cortex (SI) that is phase-locked

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doi:10.1016/j.neuroimage.2009.09.035

to the onset of the somatosensory event. It is represented by a sharp, transient increase in synchrony that is tightly time-locked to the onset of an exogenous somatosensory event and is thought to be the mechanism by which a percept is formed (Engel et al., 2001; Fell et al., 2003; Varela et al., 2001). Although this response can be modulated by top-down processes, its appearance depends upon an external, stimulus-driven sensory event. A somatosensory stimulus can also change the synchrony of ongoing, endogenous oscillations. It may generate an event-related desynchronization (ERD) or event-related synchronization (ERS) of cortical rhythms within a particular frequency range. ERD and ERS are non-phase-locked responses and vary from trial to trial, occurring at slightly different times following the stimulus event. ERD and ERS can also occur prior to a known stimulus event and it is believed that these oscillations are easily influenced by cognitive processes such as attention, orienting, and anticipation (Neuper et al., 2006; Sochurkova et al., 2006; Stancak, 2006). Although both phase-locked and non-phase-locked activities reflect changes in neural synchrony, they are thought to be functionally distinct processes in neural communication.

To our knowledge, there have been no studies that have specifically examined phase-locked versus non-phase-locked oscillations in SI during selective attention. Moreover, previous studies have not compared these to oscillations further downstream in the secondary somatosensory cortex (SII). Thus, the current study aimed to characterize attentional effects on both power and phase in SI and SII in adults who received passive somatosensory stimulation.

Materials and methods

Participants

Twelve healthy, right-handed adults (6F) were recruited from a hospital newsletter advertisement. The mean age of the participants was 28.3 ± 3.1 SEM years. Participants were screened with a telephone-based Intake Screening Questionnaire (for psychopathology and education level). Participants were excluded if they (1) reported a current mental health disorder, (2) had a history of neurological disorders, or (3) had any head injury involving the loss of consciousness.

Equipment

A 151 channel MEG system (VSM MedTech Ltd., Vancouver, Canada) was used to measure somatosensory fields. Participants lay supine with their head resting in the MEG helmet in the magnetically shielded room. The MEG signals were filtered with an online bandpass of 0.3–300 Hz and recorded at a 1250 Hz sampling rate. Head position in relation to the MEG sensors was determined by measuring the magnetic field generated by three fiducial reference coils just before and after each experimental session. T_1-weighted structural magnetic resonance images (MRI) (axial 3D spoiled gradient echo sequence) were obtained for each participant using a 1.5 Tesla Signal Advantage system (GE Medical Systems, Milwaukee). During MRI data acquisition, three radiographic markers were positioned at the same anatomical landmarks as the fiduciary coils to allow coregistration of the MEG and MRI data. Single equivalent current dipole (ECD) models were also fit to the N20 m median nerve responses in order to confirm coregistration accuracy.

Paradigms

Stimuli were non-painful, 0.2 ms pulses of electrical current, just above motor threshold (eliciting a small, passive, thumb twitch) applied cutaneously to the right median nerve. Stimuli were presented with a constant stimulus onset of 670 ms, in trains of four consecutive events followed by a pause of 1340 ms before the onset of the next train of stimuli. Participants were presented with 200 trains of stimuli over a 12-min experiment. Stimulus presentation was controlled by Presentation Software (Neurobehavioral Systems, Inc., Albany, CA). Stimuli were presented under the following two experimental conditions, counterbalanced for condition order. (1) Attend to MNS: participants were instructed to attend to the electrical stimuli and count the number of stimulus trains. To ensure eyes remained open and head remained still, participants were asked to focus on a yellow circle (2 in. diameter, 4 ft above MEG helmet). (b) Ignore MNS: participants were instructed to ignore the median nerve stimuli and attend to a video ("Pingu the Penguin") that was presented, without sound, on a back-projection screen via two mirrors, on a screen 75 cm in front of the participants. To ensure attention was directed to the video during this condition, participants were asked to count the number of times the penguin trumpeted (32 events) and the number of times he caught a fish (8 events) (both were random events interspersed throughout the video). All participants reported the correct number of incidents with an error rate of ±6% indicating that they were able to comply with instructions and successfully direct attention to the designated events at a behavioural level.

This study was approved by the Institutional Research Ethics Board and informed written consent was obtained for each participant. Additionally, it was in compliance with national legislation and the Code of Ethical Principles for Medical Research Involving Human Subjects of the World Medical Association (Declaration of Helsinki).

Data analyses

Spatial localization of cortical oscillations was performed using a spatial filtering (beamforming) approach and time–frequency analysis applied to the time course of neural activity at the identified locations of peak activity within predetermined frequency bands.

Beamformer spatial analysis

Initial spatial analyses were performed based on a minimum-variance beamformer method (synthetic aperture magnetometry: SAM (Robinson and Vrba, 1999)), by computing spatial filters from the single-trial data filtered from 1–200 Hz. We used a scalar version of the minimum-variance beamformer algorithm that estimates a single optimal current orientation at each voxel (Cheyne et al., 2007; Sekihara et al., 2004). Changes in source power were computed using the SAM pseudo-t statistic (Robinson and Vrba, 1999) which involved subtracting source power in the control period prior to stimulus presentation (−200 ms to 0 ms relative to stimulus onset) from an active period (0–200 ms post-stimulus (or gap onset)). This allowed us to identify peak locations of broad-band increases in activity to the somatosensory stimulus in the SAM images for further analysis.

Virtual sensor analyses

Based on the peak SI and SII locations as determined with SAM, we created single-trial time series of source activity or 'virtual sensors' by passing broad-spectrum (1–200 Hz) single-trial MEG signals through the spatial filter for each of the locations. This produced time series representing the averaged changes in source power for both phase-locked response and non-phase-locked responses of SI and SII over time.

Group virtual sensor analyses

Virtual sensors for SI and SII locations were also averaged across participants. To determine statistical differences in amplitude and latency between conditions, we performed repeated measures ANOVAs separately for SI and SII data to examine main effects of