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Research Report

Theta modulation of inter-regional gamma synchronization during auditory attention control

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ABSTRACT

Synchronization of gamma oscillations among brain regions is relevant for dynamically organizing communication among neurons to support cognitive and perceptual processing, including attention orienting. Recent research has demonstrated that inter-regional synchronization in the gamma-band is modulated by theta rhythms during cortical processing. It has been proposed that such cross-frequency dynamics underlie the integration of local processes into large-scale functional networks. To investigate the potential role of theta-gamma mechanisms during auditory attention control, we localized activated regions using EEG beamformer analysis, and calculated inter-regional gamma-band synchronization between activated regions as well as modulation of inter-regional gamma-band synchronization by the phase of cortical theta rhythms. Abundant synchronization of gamma-band oscillations among regions comprising the auditory attention control network was observed. This inter-regional gamma synchronization was modulated by theta phase. These results provide further evidence implicating inter-regional gamma-band synchronization, and theta-gamma interactions, in task-dependent communication among cortical regions, and provide the first evidence that such mechanisms are relevant for auditory attention control.

1. Introduction

Converging lines of evidence from noninvasive electroencephalographic (EEG) and magnetoencephalographic (MEG) recordings in humans, as well as from implanted electrodes in animals, have implicated gamma-band phase synchronization between cortical regions in visual attention (Buschman and Miller, 2007; Doesburg et al. 2008; Gregoriou et al., 2009; Siegel et al., 2008). Synchronization among brain regions has been proposed as a mechanism mediating the dynamic assignment of functional connectivity to support enhanced processing of attended information (Fries, 2005). This interpretation is consistent with previous research linking gamma synchronization among brain regions to integrative network dynamics

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supporting the performance of a particular cognitive task (Sarnthein et al. 1998; Supp et al. 2007) or binding the features of an object (Doesburg et al. 2009a; Engel et al. 1991; Gray et al. 1989; Rodriguez et al. 1999; Rose and Büchel, 2005; Rose et al., 2006; Sarnthein et al. 1998). Changes in inter-regional gamma-band synchronization, computed from intracranial data collected from humans, have been observed during the performance of a cognitive task (Fell et al. 2006) and during changes in sleep state (Fell et al. 2003). The view that neuronal coherence is a mechanism for dynamically assigning functional connectivity in the brain also garners support from evidence linking inter-regional gamma-band synchronization to increased information exchange in the cortex (Womelsdorf et al. 2007).

Experimental evidence also indicates that modulation of cortical gamma rhythms by theta oscillations plays an important role in task-dependent cortical processing (Canolty et al., 2006; Demiralp et al. 2007; Jensen and Colgin, 2007; Sauseng et al. 2008; Schack et al. 2002). It has been proposed that gamma synchrony may relate to local integration, whereas theta rhythms pertain to long-distance functional coupling in the brain (von Stein and Sarnthein, 2000). Interplay among theta and gamma rhythms, moreover, has been purported to underpin organization of information in cortical circuits to support cognition (Ward 2003), and theta and gamma oscillations emerge from highly interrelated neurophysiological mechanisms that are critical for brain function (Llinás et al. 2005). From such a vista it would appear that coupling between theta and gamma oscillations is relevant for the integration of local neuronal processes into large-scale functional brain networks. This view is buttressed by findings that low frequency (3 Hz) modulation of inter-electrode gamma-band covariance has been associated with conscious recollection (Burgess and Ali, 2002), and that gamma-band phase locking between cortical regions during visual perception is modulated by the phase of cortical theta oscillations (Doesburg et al. 2009a).

Observations that inter-regional gamma-band synchronization is involved in attention control, and that gamma synchrony among brain regions is modulated by theta oscillations during cognitive processing, lead to the hypothesis that theta rhythms will modulate gamma-band synchronization between activated brain regions during attention control. To test this we seeded dipoles in regions identified as subtending auditory attention control, using data previously published in Green et al. 2011, and derived the time series of activations at those locations in order to investigate inter-regional gamma-band synchronization within the attention control network and modulation of inter-regional gamma-band synchronization by theta phase during attention orienting. In order to isolate brain responses pertaining to the control of auditory attention, we compared neural activity on trials in which subjects shifted auditory attention in space to trials on which subjects were not required to shift attention.

2. Results

2.1. Behavioral results

Participants performed an auditory attention task wherein on each trial they were instructed to orient their attention from the center fixation cross to the left or right side of auditory space (shift-cue trials), or not to orient attention (neutral cue trials) (Fig. 1). Participants were faster to respond to target sounds on valid-cue trials (M = 694 ms, SD = 102 ms) than on either invalid-cue (M = 716 ms, SD = 106.8 ms) or neutral-cue (M = 718 ms, SD = 106.4 ms) trials. There was a main effect of cue type on reaction time (p = 0.006) without any corresponding changes in discrimination accuracy (p = 0.99), indicating that participants did shift attention to the cued location in preparation for the target. Thus, we may assume that during the cue-target interval on shift-cue trials participants were occupied in shifting attention from the fixation point to the appropriate side of the display in preparation for the upcoming target. See the original study by Störmer et al. 2009, where those results were initially published, for a more comprehensive behavioral analysis.

2.2. Beamformer source localization

Beamformer source localization revealed statistically significant (p < 0.01) bilateral activation of the superior temporal gyrus (STG), superior parietal lobule (SPL), inferior parietal lobule (IPL), and inferior frontal gyrus (IFG) during the cue-target interval for shift-cue trials, relative to neutral-cue trials. The Talairach coordinates (x, y, z) of cortical generators underlying auditory attention control were: STG = ±55, −25, 12; SPL = ±25, −55, 61; IPL = ±48, −55, 34; IFG = ±48, 38, 10. Locations of peaks of statistically significant activations are presented in Fig. 2. Additional detail regarding the results of the beamformer source localization is available in Green et al. 2011, where those findings were originally published.

2.3. Gamma-band inter-regional synchronization and activation

Auditory attention orienting was associated with significant task-dependent increases in inter-regional gamma-band synchronization between auditory cortex and parietal cortices (STG–SPL; STG–IPL), between activated parietal regions (SPL–IPL) and between frontal and parietal cortices (IPL–IFG; SPL–IFG). Gamma-band synchronization among brain regions was centered at various frequencies within the 30–50 Hz frequency range, depending on the source pair, and multiple instances of

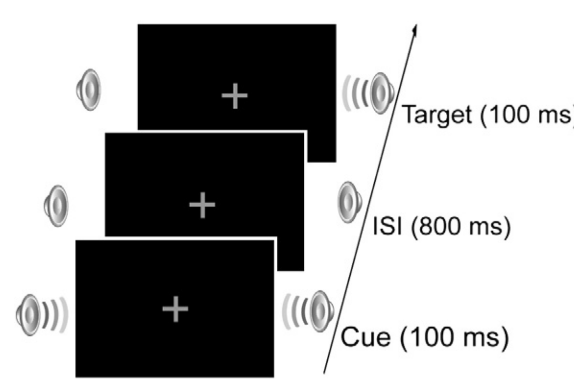

Fig. 1 – The stimulus display and its time course on a single trial.