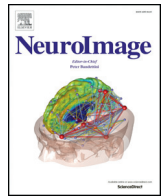




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Different coupling modes mediate cortical cross-frequency interactions

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ABSTRACT

Cross-frequency coupling (CFC) has been suggested to constitute a highly flexible mechanism for cortical information gating and processing, giving rise to conscious perception and various higher cognitive functions in humans. In particular, it might provide an elegant tool for information integration across several spatiotemporal scales within nested or coupled neuronal networks. However, it is currently unknown whether low-frequency (theta/alpha) or high-frequency gamma oscillations orchestrate cross-frequency interactions, raising the question of who is master and who is slave. While correlative evidence suggested that at least two distinct CFC modes exist, namely, phase-amplitude-coupling (PAC) and amplitude-envelope correlations (AEC), it is currently unknown whether they subservise distinct cortical functions. Novel non-invasive brain stimulation tools, such as transcranial alternating current stimulation (tACS), now provide the unique opportunity to selectively entrain the low- or high-frequency component and study subsequent effects on CFC. Here, we demonstrate the differential modulation of CFC during selective entrainment of alpha or gamma oscillations. Our results reveal that entrainment of the low-frequency component increased PAC, where gamma power became preferentially locked to the trough of the alpha oscillation, while gamma-band entrainment enhanced AECs and reduced alpha power. These results provide causal evidence for the functional role of coupled alpha and gamma oscillations for visual processing.

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1. Introduction

Cognition and conscious perception are thought to arise from neuronal interactions between functionally specialized but widely distributed cortical regions (Siegel et al., 2012). While phase synchronization between task-relevant cortical areas might integrate information across several spatial scales (Fries, 2005), cross-frequency coupling (CFC) has been suggested to constitute a flexible mechanism for information integration across temporal scales (Canolty and Knight, 2010). Hence, it might serve as a key mechanism for selective gating and processing of information within coupled or nested cortical networks and thus, subservise numerous cognitive functions in humans (Canolty and Knight, 2010; Engel et al., 2013; Voytek et al., 2010). However, the functional role of CFC is currently extensively under debate, given that (I) various methodological constraints hamper its interpretation (Aru

et al., 2014), (II) the evidence supporting its role for cognitive processing was only correlative in nature (Canolty and Knight, 2010; Voytek et al., 2010), and (III) it remained unclear whether different coupling modes (e.g. PAC or AEC) subservise distinct cortical functions. In particular, alpha–gamma PAC has been suggested to constitute a powerful mechanism to organize visual processing (Jensen et al., 2014; Spaak et al., 2012), while theta–gamma PAC might subservise memory processes and long-range cortico-cortical communication (Axmacher et al., 2010; Canolty and Knight, 2010; Lisman and Jensen, 2013; Tort et al., 2009). Most studies focused on PAC (Canolty and Knight, 2010; Voytek et al., 2010), where gamma power is preferentially phase-locked to the trough of the theta (4–7 Hz) or the alpha (8–12 Hz) rhythm. So far, it remained elusive whether the fast or the low-frequency spectral component drives their interaction (Jiang et al., 2015; Schroeder and Lakatos, 2009; Spaak et al., 2012).

In addition, it has recently been observed that the cerebral cortex exhibits a large-scale correlation structure which is independent from phase-locked signaling and can best be analyzed by quantifying AEC (Engel et al., 2013; Hipp et al., 2012). While first applied to uncover envelope correlations within one frequency range, AEC can also be applied to the cross-frequency domain (Helfrich et al., 2014a). Fig. 1A depicts a schematic how both CFC measures (PAC and AEC) can be obtained from raw data.

Abbreviations: AEC, Amplitude envelope correlations; ANOVA, Analysis of variance; EEG, Electroencephalography; CFC, Cross-frequency coupling; ICM, Intrinsic coupling mode; PAC, Phase-amplitude coupling; tACS, Transcranial alternating current stimulation.

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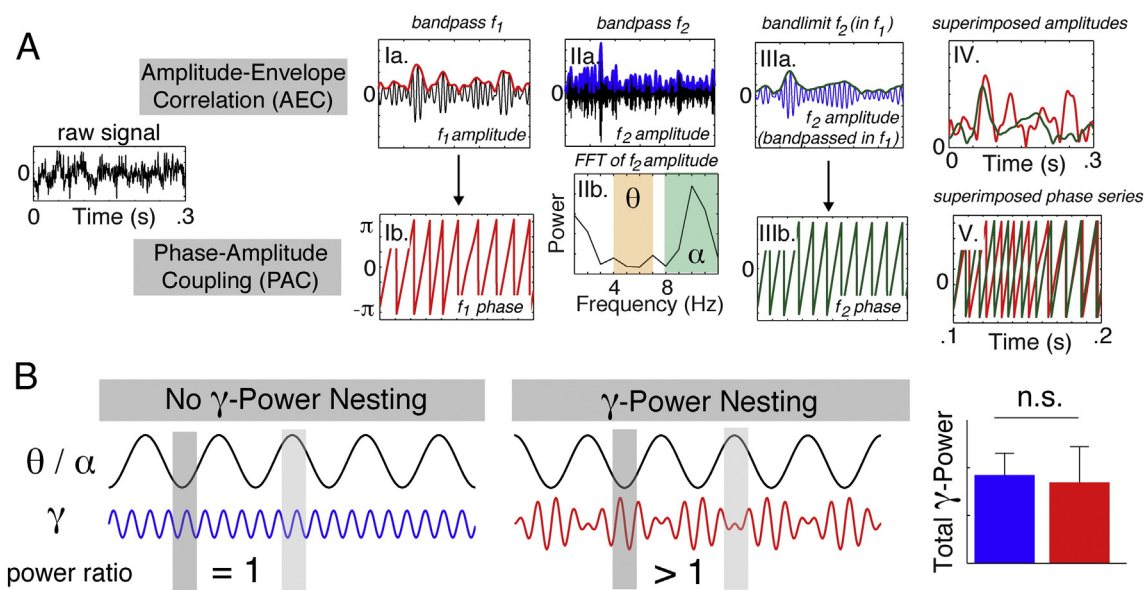


Fig. 1. Schematic illustration of CFC analysis. (A) Ia. Low-frequency (f_1) band-pass filtered signal (black) and the corresponding envelope (red) and instantaneous phase (Ib.). IIa. Gamma band-pass (f_2) filtered signal (black) and the corresponding envelope (blue). IIb. Fast Fourier transform (FFT) of the gamma envelope indicates that lower-frequency components modulate the instantaneous gamma amplitude. Shaded areas highlight theta (orange, 4–7 Hz) and alpha (green, 8–12 Hz) frequency ranges that were utilized for subsequent analyses. IIIa. The gamma envelope (blue, f_2) was filtered again in the low-frequency range (f_1) and then its envelope (green) and phase (IIIb.) were extracted. IV. Superposition of low-frequency amplitude (Ia.) and gamma envelope (IIIa.), which were then used for AEC analysis by means of Pearson's linear correlation coefficient (Fisher-Z-transformed). V. Superposition of low-frequency phase (Ib.) and the phase of the band-pass filtered gamma amplitude (IIIb.). Their interaction was analyzed by means of the phase-locking value (PLV; Voytek et al., 2010) to obtain the PAC. (B) Schematic of the relationship of the low-frequency (theta/alpha) and the gamma oscillation to illustrate the nesting effect, i.e. that the gamma amplitude is modulated by low-frequency fluctuations. Note that absolute power values averaged across all time points do not differ between conditions. However, in the case of nesting, gamma power becomes preferentially locked to the trough of the low-frequency oscillation, and thus, the distribution of gamma power changed on a shorter time scale (i.e. within an oscillatory cycle of the low-frequency oscillation). The power ratio was calculated as trough-locked gamma power (shaded dark gray) divided by the peak-locked gamma power (shaded light gray).

To investigate the mechanisms underlying the alpha–gamma interplay, we took advantage from a novel non-invasive brain stimulation technique, namely, transcranial alternating current stimulation (tACS; Herrmann et al., 2013; Thut et al., 2011), which has recently been demonstrated to selectively entrain neuronal oscillations within canonical frequency boundaries (Helfrich et al., 2014b; Ozen et al., 2010). Thus, this approach provided the unique opportunity to selectively drive one spectral component and study subsequent cross-frequency effects in coupled frequency bands. Here, we reanalyzed data from two combined tACS-EEG (electroencephalography) studies on visual perception, which was obtained during stimulation. Our aim was to study how cross-frequency interactions were modulated when either alpha (8–12 Hz; Helfrich et al., 2014b) or gamma (>35 Hz; Helfrich et al., 2014a) oscillations were entrained by tACS, i.e., when one of these processes was set up as the master through synchronization to the external driving force.

2. Material and methods

2.1. Participants

A total of 30 healthy, right-handed participants were recruited from the University of Oldenburg, Germany, and the University Medical Center Hamburg-Eppendorf, Germany. Sixteen subjects (8 female; mean age: 24.6 ± 2.8 years; 2 excluded due to technical difficulties during data acquisition) participated in study 1 and fourteen subjects (7 female; mean age: 27.5 ± 6.7 years) participated in study 2. All participants reported no history of neurological or psychiatric disease and were medication free during the experiments. They all had normal or corrected-to-normal vision and provided written informed consent according to the local ethics committee approval and the Declaration of Helsinki.

2.2. General procedure

All volunteers participated in one or two sessions of the experiments carried out within 1 week. After preparation of EEG and tACS electrodes, participants completed a training session to familiarize the volunteers with the visual stimuli to ensure adequate task performance. Participants reported their percepts by button presses with their right hand. Then all participants were familiarized with skin sensations and phosphene, which have been reported in previous tACS studies (Kanai et al., 2010; Schutter and Hortensius, 2010). However, all participants indicated that the stimulation intensity was below skin sensation and phosphene threshold. In both studies, the sham condition preceded active stimulation to avoid carry-over effects (Neuling et al., 2013).

2.3. Data acquisition

2.3.1. EEG recordings

All experiments were conducted with participants seated comfortably in a recliner in a dimly lit, electrically shielded room to avoid line noise interference. EEG electrodes were mounted in an elastic cap (EasyCap, Herrsching, Germany) prepared with a slightly abrasive electrolyte gel (Abralyt 2000, EasyCap, Herrsching, Germany). EEG recordings (impedances <20 k Ω , referenced to the nose tip) were obtained using BrainAmp amplifiers (Brain Products GmbH, Gilching, Germany) from 59 electrodes in study 1 and 31 electrodes in study 2. Signals were sampled at 1000 or 5000 Hz, amplified in the range of ± 16.384 mV at a resolution of 0.5 μ V and stored for offline analyses.

2.3.2. Electrical stimulation

In accordance with current safety limits (Nitsche et al., 2008), transcranial stimulation was applied by a battery-operated stimulator (DC-Stimulator Plus, NeuroConn, Ilmenau, Germany) via two rubber

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