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Increased phase synchronization during continuous face integration measured simultaneously with EEG and fMRI

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HIGHLIGHTS

- Using a visual binding task as example, this study presents a method to measure the amount of EEG gamma zero-lag phase synchronization and to locate its underlying regions with fMRI.
- We found an increased amount of gamma zero-lag phase synchronization during FACE compared to NOFACE with positive BOLD correlates in the left and right middle fusiform gyrus and the left precuneus.
- We thus suggest that the difference in gamma band phase between remote regions of the human visual system shifts toward zero during visual binding and can be measured with simultaneously acquired EEG/fMRI.

ABSTRACT

Objective: Gamma zero-lag phase synchronization has been measured in the animal brain during visual binding. Human scalp EEG studies used a phase locking factor (trial-to-trial phase-shift consistency) or gamma amplitude to measure binding but did not analyze common-phase signals so far. This study introduces a method to identify networks oscillating with near zero-lag phase synchronization in human subjects.
Methods: We presented unpredictably moving face parts (NOFACE) which – during some periods – produced a complete schematic face (FACE). The amount of zero-lag phase synchronization was measured using global field synchronization (GFS). GFS provides global information on the amount of instantaneous coincidences in specific frequencies throughout the brain.
Results: Gamma GFS was increased during the FACE condition. To localize the underlying areas, we correlated gamma GFS with simultaneously recorded BOLD responses. Positive correlates comprised the bilateral middle fusiform gyrus and the left precuneus.
Conclusions: These areas may form a network of areas transiently synchronized during face integration, including face-specific as well as binding-specific regions and regions for visual processing in general.
Significance: Thus, the amount of zero-lag phase synchronization between remote regions of the human visual system can be measured with simultaneously acquired EEG/fMRI.

1. Introduction

How neural activity is coordinated to create unified visual percepts is still one of the critical questions in neuroscience. This aspect of the so-called binding problem exists because different visual aspects are processed both independently and at remote cortical sites (Billock and Tsou, 2004). The visual binding problem has been studied in cat primary visual cortex using single cell recordings. There, neuron firing rates as well as local field potentials of near 40 Hz frequencies (gamma) synchronized with a precision in the millisecond range to accomplish feature integration (Gray and Singer, 1989). Signals synchronized with a common phase between hemispheres and over different visual hierarchy levels (Gray et al., 1989). Such synchronization is believed to be internally generated in the cortex not externally caused by stimulus-locked changes in amplitude or discharge rate (Singer, 1999). Zero-lag phase synchronization in the gamma range was also found in anesthetized cats, indicating possible automatic processing of visual binding stimuli (Brecht et al., 1999; Gray and Singer, 1989).

In this study, we investigated whether the zero-lag phase synchronization found in animals could be transferred to a system level using extracranial EEG recordings in human subjects. We

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attempted to demonstrate that, in humans, face elements are bound to an entire facial percept with a high amount of zero-lag phase synchronization and that this can be measured with EEG. Thus, we applied a global measure of the amount of zero-lag phase synchronization (global field synchronization – GFS) over the whole scalp (Koenig et al., 2001).

To date, no study has analyzed the visual binding process by focusing on synchronization of oscillations with no phase difference. Although Rodriguez et al. (1999), on a descriptive level, reported zero-lag phase synchronization during the perception of Mooney faces, their main focus was on the phase locking factor, a measure of phase shifts' stability. The authors did not elaborate further on observations of zero-lag phase synchronization between signals. Other visual binding studies also explored this phase locking factor between pairs of electrodes (Gruber et al., 2002, 2006; Herrmann et al., 1999; Lachaux et al., 2005, 1999; Melloni et al., 2007; Tallon-Baudry et al., 1997; Uhlhaas et al., 2009; Von der Malsburg, 1995). In several EEG studies, gamma oscillations were studied using amplitude measures of the induced gamma band response (e.g. Freunberger et al., 2007). Some of these studies used rotating faces (Keil et al., 1999) or stable Mooney faces (Grützner et al., 2010; Uhlhaas et al., 2009) as stimulus material.

Another novelty of our study is the experimental face integration paradigm applied here, specifically designed to analyze internally generated ongoing oscillations in the gamma range. Since stimulus onsets have been hypothesized to induce EEG phase-resets (Makeig et al., 2002), we removed a potentially confounding clear stimulus onset from our stimulus material. Instead, we showed randomly moving elements of a schematic face (NOFACE) starting to produce a facial percept (FACE) at subjectively unpredictable instants. The order of FACE and NOFACE trials was pseudo-randomized; exact time points when subjects started to perceive an entire face were unknown due to the randomized movement of the face elements and inter-subject, as well as inter-trial, variability. In both FACE and NOFACE conditions, elements were always present; only their constellation allowed for the occasional percept of a whole face, so that binding was the only process distinguishing the FACE from the NOFACE condition. This experiment was a passive viewing task allowing measurement of the visual binding process in ongoing EEG without disruptions from either motor reactions or expectancy biases.

In this study, we define binding according to Gray and Singer (1989) as the ability of the brain to relate spatially separate features to each other in a way that they form a new unitary visual percept. This is expected to be the case in the FACE condition, where the face parts from the unitary percept of a face. In other studies, the presentation of a single contour (Singer, 1999, review article), meaningful (Gruber et al., 2006) or familiar stimuli (Supp et al., 2007) or faces (Rodriguez et al., 1999) have been defined as conditions representing visual binding processes, while the presentation of different contours moving in different directions or the presentation of meaningless shapes represented unbound conditions. In our experiment, the binding condition is reflected by the parts forming a face (FACE condition), while the unbound condition is given by the single parts moving around randomly and thus representing meaningless features. Billock and Tsou (2004) formulated that an interesting failure of the binding process would be the loss of the physical unity of an image. In this experiment, we tried to represent this failure by disrupting the face percept in the NOFACE condition.

We deliberately based our analyses on global EEG features, because we wanted to avoid ambiguities due to volume conduction. Our method – GFS – is a global measure of the relative amount of zero-lag phase synchronization across all electrodes at a given frequency independent of an eventual locking of EEG oscillations to a stimulus. GFS does not make any assumptions about the location of the synchronized activity; therefore, to identify networks containing synchronized regions, we combined these global GFS values with blood oxygen level dependent (BOLD) responses. The relationship between gamma phase synchronization and fMRI BOLD responses has not yet been analyzed. However, gamma amplitudes have consistently been shown to correlate positively with BOLD signals, as first evidenced in the visual cortices of animals (Goense and Logothetis, 2008; Niessing et al., 2005). More recently, this correlation was demonstrated in human subjects; Koch et al. (2009) conducted a simultaneous EEG and near-infrared spectroscopy study looking at gamma oscillations from occipital electrodes while subjects viewed moving gratings. Martuzzi et al. (2009) and Zaehle et al. (2009) showed positive correlations of gamma and BOLD responses to visual tasks, applying both methods separately. Few studies reporting positive correlations between gamma power and BOLD responses with different tasks have simultaneously measured EEG gamma activity and BOLD responses (Michels et al., 2010; Mulert et al., 2010; Scheeringa et al., 2011). Some studies have analyzed face perception using simultaneous EEG and fMRI, but they examined the relationship between event related potentials and BOLD responses (Corrigan et al., 2009; Sadeh et al., 2010, 2008).

We followed two hypotheses in this study. First, we hypothesized that gamma phase synchronization in the gamma range around 40 Hz would increase during the perception of a whole face, consistent with the findings of zero-lag phase synchronization in this frequency range in animal visual cortices (e.g. Gray and Singer, 1989). Second, the combination of EEG and fMRI should yield deeper insight into the relationship between gamma phase synchronization and hemodynamic responses during visual binding. Here, we expected a positive correlation of gamma phase synchronization and BOLD responses in the areas most important for visual binding and face perception. These include, on one hand, parietal areas relevant for visual binding in general (Himmelbach et al., 2009) and, on the other hand, areas associated with face perception such as the middle fusiform gyrus (mFG) (Fairhall and Ishai, 2007; Haxby et al., 2001; Tsao and Livingstone, 2008). In this study, standard BOLD–GLM contrasts were performed primarily to show that our task-induced BOLD responses occurred in areas that would be expected for face processing and for the processing of moving visual stimuli. According to the literature, we expected a right-lateralized pattern of regions responding to the FACE compared with the NOFACE condition, since previous studies have shown consistently stronger right hemispheric responses to face stimuli (Fairhall and Ishai, 2007; Haxby et al., 1999; Kanwisher et al., 1997; Rossion et al., 2000).

The results met our assumptions and are intended to extend the current knowledge and methodology related to transient electrophysiological oscillations in response to feature integration.

2. Methods

2.1. Subjects

Fourteen healthy subjects (seven females; age $M = 27.29$, SD = 2.5 years) recruited via university message boards were studied using simultaneous EEG/fMRI. All of the subjects had normal or corrected-to-normal vision, all met the standard fMRI inclusion criteria and gave their written informed consent to participate in the study. None of the subjects suffered from neurological or psychiatric disorders or used psychoactive medication or drugs. The subjects refrained from caffeine, alcohol and nicotine for six hours before the measurement. The tests were run during early morning hours to help control the circadian rhythm effects. The local ethics committee of Bern, Switzerland approved the study.

2.2. Stimuli and task

In the past, different stimuli have been used to induce specific gamma band oscillations. To obtain local changes in amplitude in