Neuronal Networks During Repetition Priming: Information Transfer Revealed by Partial-Directed Coherence (PDC)

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Introduction

Previous findings from this study:

Repeated presentation of stimuli results in the behavioral phenomenon of priming and is commonly accompanied by a decrease of neuronal activity. Specifically, this reduction is reflected by a decrease of oscillatory brain responses in the EEG gamma-range and by lowered haemodynamic activation. These findings were extended by a joint event-related fMRI and EEG study on word/pseudoword processing [Fiebach et al., 2005].

Our EEG results revealed that the repetition effect depends on the familiarity of stimuli. Morlet wavelet analysis of EEG signals showed that the repeated presentation of words lead to reduced gamma-band responses between 200-350 ms post-stimulus onset, whereas repeated pseudowords induced gamma-band increases during the same time-window. In order to address long-range synchronization of distant positions we used the traditional measure of phase coherence, phase-locking analysis (PLA), between EEG signals [Lachaux et al. 1999, Gruber & Müller, 2005]. This EEG coupling analysis indicated the involvement of specific networks during repetition priming that are established by synchronous activation of distributed brain areas. The principal importance of oscillatory synchronization phenomena during object recognition has been shown by several studies [e.g., Tallon-Baudry, 2003; Supp et al. 2005].

Current aims of this study:

We follow a multivariate autoregressive modeling (MVAR) approach in order to investigate oscillatory dynamics of neuronal networks both, on the local scale (spectral power changes) and on the basis of long-range interactions (changes of EEG coupling values). Specifically, we

1. Quantify the oscillatory EEG responses in the gamma-range to investigate whether the MVAR-based power-spectrum is equally modulated by the factors stimulus type and repetition (1^{st} presentation of words > 2^{nd} presentation of words; 2^{nd} presentation of pseudowords > 1^{st} presentation of pseudowords).
2. Use ordinary coherence analysis to test, whether MVAR-based coherence reveal results comparable to our previous PLA findings: a decrease of phase coherence for repeated words, while repeated pseudowords show an increase of phase synchrony.
3. On the basis of the MVAR model we apply a new EEG coupling measure, partial-directed coherence (PDC), based upon Granger Causality. PDC is advantageous over other coupling measures (such as classical coherence or phase locking statistics) since it informs us whether and how two positions under study are effectively connected, rather than merely describing mutual synchronicity [Baccala & Sameshima, 2001]. In addition, confounding factors such as volume conduction or reference electrode influences are eliminated by the use of PDC, possibly leading to more developed estimates of long-range synchronization processes.

Materials & Methods

Stimuli and behavioral procedure:

14 Participants (mean: 24.2 years of age) performed a lexical decision task on 136 words and 136 pseudowords, each presented for 700 ms. 58 stimuli of each class were repeated after 5-10 trials (i.e., 20-40 s) relative to their first presentation. Words: length 4-7 letters, 1-2 syllables, mean word frequency 87.9. Pseudowords: pronounceable and orthographically regular, matched for length with words.

EEG data acquisition:

27 AgCl electrodes placed according an extended 10/20 system, nose reference, sampling rate: 500 Hz, hardware bandpass: 0.01-200 Hz.

Data analysis using multivariate autoregressive (AR) modeling :

To model the multi-channel nature of the EEG recording we fitted a multivariate AR model for five time-windows (each 150 ms in length) to each condition and each subject. In relation to stimulus-onset we selected the following time-windows (TW): -200 to -50 ms (baseline TW), 0 to 150 ms (2^{nd} TW), 200 to 350 ms (3^{rd} TW), 400 to 550 ms (4^{th} TW), 600 to 750 ms (5^{th} TW).

The MVAR model is a mathematical modeling of the EEG time series as described by

$$Y_t = \sum_{k=1}^{p} A_k Y_{t-k} + X_t$$

The vector Y_t contains the samples of all M channels at the time instance t. The matrices A_k indicate the MVAR parameters up to an order p, the off-diagonal elements represent the cross-terms between the channels. The multivariate process X_t is the so-called innovation process and is assumed to be a zero-mean white noise process with a variance-covariance matrix $\sum$; MVAR parameter estimation via multivariate Burg algorithm [Schlögl, 2006], MVAR model order p set to 15 to guarantee sufficient frequency-resolution. Frequency-transformation of MVAR-parameters yields an M x M matrix $\bar{A}(f)$ for each frequency f.

Data analysis: power changes in EEG signals

The frequency transformed matrix $Y_{ii}(f)$ elements represent the auto-spectrum or power-spectrum of channel i. The power spectral density is given by $S_Y(f) = |Y \cdot Y^x(f)|$ and is obtained by $S_Y(f) = H(f) \cdot \Sigma \cdot H^H(f)$. The superscript indicates the *Hermetian* operator (transposed complex conjugate of matrix H).

Data analysis: coherence (COH) changes in EEG signals

COH is defined as

$$COH_{ij}^2(f) = \frac{S_{ij}(f)}{\sqrt{S_{ii}(f) \cdot S_{jj}(f)}} = \frac{Y_{ij}(f) \cdot Y_{ji}(f)}{Y_{ii}(f) \cdot Y_{jj}(f)}$$

Data analysis: partial-directed coherence (PDC) changes in EEG signals

PDC can be obtained according to

$$PDC_{mn}(f) = \frac{\bar{A}_{mn}(f)}{\sqrt{\bar{A}_{:,n}^H(f)\bar{A}_{:,n}(f)}}$$

where $\bar{A}_{mn}(f)$ is the m, n-th element and $\bar{A}_{:,n}(f)$ is the n-th column of $\bar{A}(f)$. These PDC values provide information about the information flow for each electrode pair and each frequency (spectral frequency resolution: 1 Hz).

The implementation of all computational steps are available online from the open source project BIOSIG under http://biosig.sf.net (Schl□gl, 2003-2006).

Statistical evaluation:

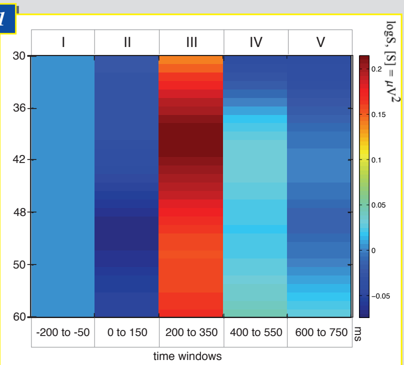
Consistent changes in power, coherence or PDC values across subjects were obtained by calculating the difference between baseline TW and all other TW for each subject. A paired t-test applied on the respective values to evaluate whether the differences of all subjects were significantly (i.e., p<0.01) above zero. To correct for multiple comparisons: False Discovery Rate (FDR) [Nolte et al. 2004].

Results

Spectral changes in response to words/pseudowords:

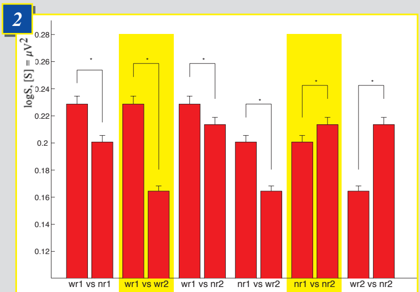
- Increase of gamma-power (peak: 38-41 Hz, range: 34-46 Hz) in the 200-350 ms (3. TW) (cf. Figure 1).
- Gamma band responses varied with the factor stimulus-type and repetition: 1^{st} word > 2^{nd} word; 2^{nd} pseudoword > 1^{st} pseudoword presentation (cf. Figure 2).

1



Grand mean baseline-corrected time-by-frequency plots in the gamma-range (30-60Hz): for each of the 5 TW the power values were averaged across electrodes and all four experimental conditions (1^{st} word, 2^{nd} word, 1^{st} pseudoword, 2^{nd} pseudoword presentation). The 3rd TW revealed a prominent increase of gamma-band power (range: 34-46 Hz).

2

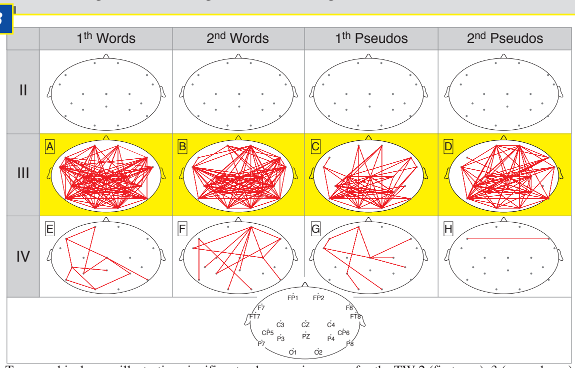


Gamma responses based on the mean peak frequency range (34-46 Hz) in the time-window between 200-350 ms (3. TW) after stimulus onset, averaged across electrode sites. Asterisk indicate statistical significance (p<0.05).

Coherence (COH) changes in response to words/pseudowords:

- The number of significant coherence values decrease for the 2^{nd} presentation of words as compared to their 1^{st} presentation (cf. Figure 3 A-B).
- The number of significant coherence values increase for the 2^{nd} presentation of pseudowords number as compared to their 1^{st} presentation (cf. Figure 3 C-D).

3

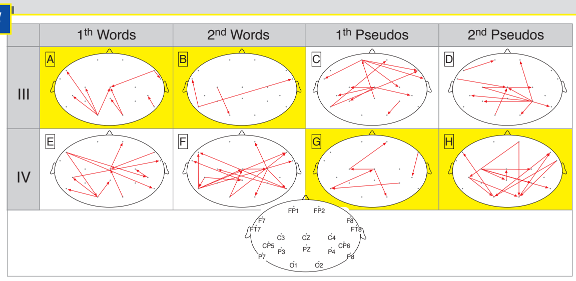


Topographical maps illustrating significant coherence increases for the TW 2 (first row), 3 (second row) and 4 (third row) in the gamma-peak frequency range (34-46 Hz). Black lines indicate significant increases (as compared to baseline) between selected recording sites (p<0.01). Corrected for multiple comparisons using FDR.

PDC changes in response to words/pseudowords:

- 3^{rd} TW: similar to the results obtained with COH; the number of PDC values decrease for 2^{nd} word- as compared to 1^{st} word-presentation (cf. Figure 4 A-B).
- 3^{rd} TW: the number of PDC values stay nearly constant (a slight decrease) for 2^{nd} pseudoword- as compared to 1st pseudoword-presentation (cf. Figure 4 C-D).
- 4^{th} TW: while the number of PDC values between 1^{st} and 2^{nd} word presentation hardly change, the contrary is the case during pseudoword processing (cf. Figure 4 E-H).

4



Topographical maps illustrating significant PDC increases for the TW 3 and 4. in the gamma-peak frequency (34-46 Hz). Lines indicate significant increases (as compared to baseline) between recording selected recording sites (p<0.01). Corrected for multiple comparisons using FDR.

Discussion

MVAR-based power-spectra: oscillatory brain activity in the gamma frequency range

- The frequency range of the mean gamma-peak in the MVAR spectrum (38-41Hz) is close to the mean gamma-peak frequency (40.43 Hz, SE: 2.54) revealed by our previous wavelet analysis.
- The level of gamma band-power is modulated by stimulus-type and repetition as seen previously in the wavelet analysis.

MVAR-based coherence (COH) : long-range synchronization patterns

- The pattern of coherence changes modulated by stimulus-type and repetition is comparable to our previous results obtained by phase-locking analysis (PLA).
  Besides the general differences of MVAR and wavelet analysis, the convergent patterns of COH and PLA are not surprising: PLA constitutes a variant of coherence, namely phase-coherence.

MVAR-based PDC: information transfer and effective connectivity

- Volume conduction and reference electrode activity are artifacts for coherence analysis and its physiologic interpretation in terms of cortical couplings: PDC avoids such confounding factors
- PDC analysis revealed a considerable number of coupling changes not only in the 3^{rd} but also in the 4^{th} TW.
- The PDC values revealed a more complex pattern. However, by considering the coupling results in both time-windows together, these patterns are in accordance with the ones previously confirmed by both, MVAR coheherence and PL-wavelet analysis.

Conclusion

- Our results indicate that MVAR analysis is a suitable approach not only to detect oscillatory brain responses in the gamma range but also to quantify long-range synchronization patterns on the basis of coherence values. The results of both measures point to the same direction as those found by wavelet analysis and PLA.
- The pattern of the PDC values modulated by the four conditions supports the hypothesis that during repetition priming specific networks are established by synchronous activation of distributed brain areas.

References:

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