Available online at www.sciencedirect.com
ScienceDirect
Neuroscience and Biobehavioral Reviews 31 (2007) 1003–1016
NEUROSCIENCE AND BIOBEHAVIORAL REVIEWS
www.elsevier.com/locate/neubiorev

Review

# Event-related phase reorganization may explain evoked neural dynamics

Wolfgang Klimesch[a,*], Paul Sauseng[a], Simon Hanslmayr[b], Walter Gruber[a], Roman Freunberger[a]

[a]*Department of Physiological Psychology, Institute of Psychology, University of Salzburg, Hellbrunnerstr. 34, A-5020 Salzburg, Austria*
[b]*Department of Psychology, University of Regensburg, Germany*

Received 10 November 2006; received in revised form 19 March 2007; accepted 29 March 2007

**Abstract**

The traditional view holds that event-related potentials (ERPs) reflect fixed latency, fixed polarity evoked responses that appear superimposed on the 'background EEG'. The validity of the evoked model has been questioned by studies arguing that ERPs are generated at least in part by a reset of ongoing oscillations. But a proof of phase reset that is distinct from the 'artificial' influence of evoked components on EEG phase—has been proven difficult for a variety of methodological reasons. We argue that a theoretical analysis of the assumptions and empirical evaluation of predictions of the evoked and oscillatory ERP model offer a promising way to shed new light on mechanisms generating ERPs that goes well beyond attempts to prove phase reset. Research on EEG oscillations documents that oscillations are task relevant and show a common operating principle, which is the control of the timing of neural activity. Both findings suggest that phase reorganization of task relevant oscillations is a theoretical necessity. We further argue and show evidence that (i) task relevant oscillations exhibit a typical interactive and task relevant relationship between pre- and poststimulus power in the theta and alpha frequency range in a way that small prestimulus power is related to large poststimulus power and vice versa, (ii) ERP (interpeak) latencies and (iii) ERP amplitudes reflect frequency characteristics of alpha and theta oscillations. We emphasize that central assumptions of the evoked model cannot be substantiated and conclude that the ERPR model offers a new way for an integrative interpretation of ongoing and event-related EEG phenomena.


*Keywords:* Alpha oscillations; Electroencephalogram (EEG); Event-related potential (ERP); Phase reset; Theta

**Contents**

1. Introduction: beyond phase reset . . . 1004
2. Brain oscillation theory and the generation of ERPs . . . 1004
    2.1. The functional meaning of oscillations . . . 1004
    2.2. Timing of neuronal activity . . . 1005
    2.3. Summary of findings establishing a brain oscillation theory . . . 1005
    2.4. Theoretical arguments for the involvement of oscillations in the generation of ERPs . . . 1006
3. Conceptual basis and assumptions of the evoked model . . . 1007
4. Conceptual basis and assumptions of the ERPR model . . . 1007
5. Evaluation of the evoked model . . . 1010
6. Evaluation of the ERPR model . . . 1011
7. Conclusions . . . 1013
References . . . 1014

*Corresponding author. Tel.: +43 662 8044 5120/5136; fax: +43 662 8044 5126.
*E-mail address:* wolfgang.klimesch@sbg.ac.at (W. Klimesch).

0149-7634/$ - see front matter 
doi:10.1016/j.neubiorev.2007.03.005

## 1. Introduction: beyond phase reset

Whether event-related potentials (ERPs) are generated by fixed latency—fixed polarity responses or by a reset of oscillatory activity is a hotly debated issue (e.g., Basar,1999a; Brandt, 1997; Barry et al., 2003; David et al., 2005; Düzel et al., 2005; Fell et al., 2004; Fuentemilla et al., 2006; Gruber et al., 2005; Hamada, 2005; Hanslmayr et al., 2007; Jansen et al., 2003; Klimesch et al., 2004a, b; Kruglikov and Schiff, 2003; Makeig et al., 2002; Mäkinen et al., 2005; Mazaheri and Picton, 2005; Mazaheri and Jensen, 2006; Naruse et al., 2006; Penny et al., 2002; Rizzuto et al., 2003; Shah et al., 2004; Tass, 2000; Yamagishi et al., 2003). In a recent review, Sauseng et al. (in press) have demonstrated that many of the arguments used to test the predictions of the evoked and phase reset model appear to be not valid, largely because of methodological problems. As an example, one important prediction of the phase reset model is empirical evidence for phase concentration in the absence of a power increase. The underlying idea is that a reset of phase will not lead to a power change, whereas the superposition of an evoked response on background electroencephalographic (EEG) activity must lead to an increase in power. Although a valid prediction, it may be argued that a power increase (due to an evoked response) may not be detected, because it may be too small to reach significance or because it may be masked by a simultaneous desynchronization (e.g., in alpha activity). Other problems are that in order to prove phase reset it would be necessary to demonstrate that an ongoing oscillation is reset and that the same neural sources are involved in both, a reset in phase and the generation of the ERP (for a detailed discussion of these and related issues see Sauseng et al., in press).

The controversy between the evoked and phase reset model is important and—by the use of new methods—may lead to important new insights into the evoked neural dynamics in the near future. In the present article, however, we argue that this controversy has (i) unnecessarily narrowed and focused the potential influence of oscillations on ERPs on only one and highly specific mechanism, namely phase reset, and even more importantly that (ii) a proof of phase reset is not a necessary requirement to distinguish the evoked model from an oscillatory model of ERP generation.

(i) There are different mechanisms other than phase reset that may have an important influence on the generation of ERPs. As an example, it is very well conceivable that an oscillation may be elicited ( = evoked) by a stimulus or an event with a preferred phase and, thus, contributes to the generation of an ERP. This case of an evoked oscillation would be characterized by a very low amplitude oscillation during a prestimulus period that would give way to an evoked oscillation with a few large amplitude cycles that contribute to the generation of an ERP. Also, ongoing oscillations might appear to contribute to the generation of ERPs even if there is no phase reset. Let us assume that a task relevant neural processing system consists of two interrelated networks capable of oscillating in the same frequency range. One network oscillates with large amplitudes predominantly during a prestimulus period when a subject prepares to respond but vanishes if a stimulus is presented and/or a task has to be processed. Another network, however, may start to oscillate with a preferred phase in response to a stimulus and/or task demand, thereby contributing to the emergence of an ERP. Finally, it is also possible that event-related phase coupling between different oscillations may lead to a transient phase alignment (between evoked and/or ongoing oscillations) that generates ERP components. We subsume these different mechanisms (including phase reset) that may contribute to the generation of ERPs under the term event-related phase reorganization (ERPR).

(ii) We argue that for the evaluation of the two models findings about the functional meaning of oscillations must be considered. The crucial question is, whether the 'background' EEG can be considered 'random noise' (as is stated by the evoked model) or consists (at least in part) of oscillatory activity that serves specific functions. In the next section we show that research on oscillations has led to specific findings and conclusions that we subsume under the term 'brain oscillation theory'. We argue that from a theoretical evaluation of these findings, ERPR can be derived as a necessary mechanism of event-related brain dynamics.

## 2. Brain oscillation theory and the generation of ERPs

There is a rich body of empirical findings about brain oscillations (for reviews see e.g. Basar, 1999a, b; Buzsaki, 2006). Here, we focus on only two aspects that are relevant for the theoretical evaluation of ERPR, the functional meaning of oscillations and their relevance for the timing of neuronal processes.

### 2.1. *The functional meaning of oscillations*

EEG oscillations have been related to a variety of divergent functions (such as sleep, perception and different types of cognitive processes, cf. Steriade, 1999; Singer and Gray, 1995; Buzsaki, 2002). Findings from the last two or three decades suggest that sensory and cognitive processes are modulated—or probably even enabled—by synchronous neural activity that is induced by oscillatory activity. Prominent examples are the functional meaning of gamma and theta oscillations for sensory coding and memory, respectively (for recent reviews cf. Herrmann et al., 2004b; Buzsaki, 2006; Kahana, 2006).

Recordings from the visual cortex demonstrate that gamma oscillations serve an important function for perception. It could be shown—originally on the basis of animal studies—that elementary visual stimulus properties ('features') induce synchronous neuronal activity (in gamma frequency with a precision in the range of