NeuroImage 103 (2014) 119–129

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

Alpha phase, temporal attention, and the generation of early event related potentials

Walter R. Gruber [a], Andrea Zauner [a], Julia Lechinger [a], Manuel Schabus [a], Rade Kutil [b], Wolfgang Klimesch [a,*]

[a] *University of Salzburg, Division of Physiological Psychology, Center of Cognitive Neuroscience, Austria*
[b] *University of Salzburg, Department of Computer Sciences, Austria*

ARTICLE INFO

Article history:
Accepted 31 August 2014
Available online 16 September 2014

Keywords:
Alpha
P_1
Temporal attention
Phase reorganization
Phase reset
Event-related potential

ABSTRACT

In the present study, we have investigated the influence of ongoing alpha phase on the generation of the P_1 component of the visual ERP, recorded in a target detection task. Our hypothesis is that in trials where pre- or peristimulus alpha phase is already aligned in a way that voltage positive alpha peaks develop seamlessly into the P_1, detection performance will be enhanced as compared to trials where alpha is not aligned. The findings supported our hypothesis and showed that target detection times for the subset of seamless alpha trials was significantly shorter than for trials that are not seamless. Our findings contradict the evoked model for the generation of early ERP components, which rests on the assumption of fixed latency, fixed polarity components. We found that in the non-seamless trials the 'candidate' component of the single trial P_1 was at the opposite polarity. Despite this fact, alpha phase locking was at the same high level as was observed for the seamless trials. Finally, we found that prestimulus alpha phase was aligned already in a time window preceding the P_1 by 400 ms.

Introduction

One of the crucial issues in EEG research concerns the question, what the processes are that generate components of event-related potentials (ERPs). With respect to the early components, two opposing models play a prominent role. The evoked model, representing the traditional view, holds that early components are generated by a (more or less) constant stimulus evoked amplitude response that appears superimposed on the ongoing EEG which represents meaningless background activity (for a summary and review of this issue, see Klimesch et al., 2006, 2007). In sharp contrast, the phase reset model assumes that ongoing oscillations undergo an event-related modulation of phase (e.g. Makeig et al., 2002; Klimesch et al., 2004a, 2004b). These questions have a long history (e.g., Basar, 1980, 1999a, 1999b; Brandt, 1997) and became hotly debated during the last ten years (e.g., Düzel et al., 2005; Fell et al., 2004; Fuentemilla et al., 2006; Gruber et al., 2005; Hanslmayr et al., 2007; Jansen et al., 2003; Klimesch et al., 2004a, 2004b, 2006; Kruglikov and Schiff, 2003; Mazaheri and Jensen, 2006; Naruse et al., 2006; Rizzuto et al., 2003; cf. Sauseng et al., 2007 for a comprehensive review).

When evaluating the controversy between the evoked and phase reset model, at least three aspects must be considered, (i) a methodological aspect and two functional aspects concerning the (ii) background EEG and (iii) ongoing oscillations. We briefly review the central arguments of this controversy.

The methodological aspect deals with the 'superposition problem' and the question, whether an evoked amplitude response can be dissociated from a phase response. The problem is that a constant (i.e. stimulus locked) evoked amplitude response (i.e. evoked component) appearing superimposed on random, ongoing oscillations mimics a phase reset, because filtering turns a transient response into an oscillation. Analyzing phase in an attempt to document a phase reset (i.e. a stimulus locked phase concentration) requires filtering. But there is no way to decide whether a phase concentration is due to a real phase reset or to an evoked component. Many different attempts have been made to solve the superposition problem. Just to mention one example, Mäkinen et al. (2005) have suggested to use amplitude variance (instead of phase concentration) to distinguish a real from an artificial phase reset. The basic idea is that in the case of a real phase reset amplitude variance should approach zero because a phase reset without an amplitude response will abolish any intertrial variance in amplitudes during the time window of a phase reset. On the other hand, if the ERP is generated by an evoked amplitude response, a constant amplitude is added to ongoing, random oscillations. Because, the polarity of the oscillations (representing the background EEG) varies (according to the evoked model) randomly in relation to the evoked response, the variance underlying the ERP will increase. But the problem here is that a realistic phase reset model has to assume that amplitudes will also be modulated. Research on event related desynchronization/synchronization (ERD/ERS) has shown consistently that different frequency bands respond with a decrease or increase in

---

[*] Corresponding author at: University of Salzburg, Division of Physiological Psychology, Department of Psychology and Center of Cognitive Neuroscience, Hellbrunnerstr. 34, A-5020 SALZBURG, Austria. Fax: +43 662 8044 5126.
E-mail address: Wolfgang.Klimesch@sbg.ac.at (W. Klimesch).

http://dx.doi.org/10.1016/j.neuroimage.2014.08.055
1053-8119/

amplitudes (i.e. with ERD or ERS; for reviews see e.g., Klimesch, 1999). And the problem is that a real phase reset on which a variable event-related increase in amplitudes (ERS) is superimposed will also lead to an increase in amplitude variance. The general conclusion from these and related discussions was that the superposition problem cannot be solved (for a detailed argumentation and review, cf. Sauseng et al., 2007) and that the predictions of the phase reset and evoked model cannot be differentiated if data analysis is based on filtering and on that time window (poststimulus) in which the ERP is generated.

Despite this methodological problem, the phase reset and evoked model can indeed be differentiated when considering the ongoing EEG and the relationship between the pre- and poststimulus EEG. The reason is that the evoked model makes a clear assumption about the ongoing EEG which is considered ‘background’ EEG reflecting random voltage fluctuations. The general prediction, thus, is that the ongoing EEG – including ongoing oscillations – should be functionally meaningless. But research on EEG oscillations has meanwhile clearly documented that they play an important role physiologically and psychologically (for reviews cf. e.g., Buzsáki, 2006; Jensen et al., 2012; Klimesch, 1999; Lopes da Silva, 2013). In addition, a variety of consistent and functionally important relationships have been found between the pre- and poststimulus EEG. As an example, it has been shown that prestimulus power in the theta and alpha frequency bands is associated with cognitive performance (e.g. Hanslmayr et al., 2005). Thus, evidence for the functional meaning of background EEG allows rejecting the evoked model at least in its most radical formulation.

The most convincing evidence for the influence of phase on the generation of early ERP components comes from research on the influence of ongoing oscillations on perception and/or the phase of early ERP components. Within this research approach, phase reset is just one – and possibly unrealistic example – of an event related phase response. There are other mechanisms, particularly prestimulus phase alignment (Fellinger et al., 2012) or asymmetric modulations of oscillatory amplitudes (Mazaheri and Jensen, 2008; Nikulin, et al., 2007; for a review on these and related issues cf. Klimesch et al., 2007) that influence early stages of stimulus processes and ERP components.

A variety of studies have shown that the phase of alpha oscillations during the time window of visual stimulus presentation (peristimulus alpha phase) has an influence on the processing of the stimulus (Busch et al., 2009; Busch and VanRullen, 2010; Callaway and Yeager, 1960; Dustman and Beck, 1965; Mathewson et al., 2009; Varela et al., 1981; VanRullen et al., 2006; for a review see Hanslmayr et al., 2011). As an example, in an early study by Callaway and Yeager (1960) it was found that the positive peristimulus alpha phase is associated with shorter reaction times RTs. Mathewson et al. (2009) have also observed that the phase of alpha at stimulus onset was different for detected as compared to undetected trials (cf. Busch et al., 2009 for similar findings). In the case a target could not be detected, a negative peak at stimulus onset was associated with significantly reduced P_1 amplitude.

The interesting hypothesis that can be derived from these findings is that in trials where the pre- and peristimulus phases of alpha at stimulus onset develop seamlessly into the P1 component, a stimulus is more likely to be detected as in trials where alpha is in counter-phase. The reason, underlying this hypothesis, is that alpha plays an important role for temporal attention (Klimesch, 2012) and that the enhancing function of temporal attention is seen in the facilitation of an early categorization processes of the presented stimulus that most likely takes place in the time window of the P1 (Klimesch, 2011). Thus, it is important to note that the alignment of phase is expected to occur with respect to the time window of the P1, but not with respect to stimulus onset.

Research on the influence of alpha phase on the attentional blink (AB) phenomenon is in line with the suggested hypothesis. The AB phenomenon is the reduced ability to report a second target after identifying a first target in a rapid serial visual presentation (RSVP) of stimuli (e.g., letters). Stimuli are presented at approximately 10 items per second which means that the presentation frequency is in the alpha range. In the AB paradigm, subjects are instructed to search for two targets, T1 and T2. The typical finding is the failure to report T2 in about 50% of the cases if the preceding T1 stimulus could be identified. In a study by Zauner et al. (2012) it could be shown that the inability to report T2 is associated with a negative polarity alpha phase entrainment peristimulus to T2. This suggests that a negative polarity of alpha during stimulus presentation (of T2) may be responsible for the failure to report T2 because ongoing alpha is in counter-phase relative to the appearance of the P_1.

The present study was designed to test the suggested hypothesis by analyzing ongoing alpha phase relative to the peak latency of the P_1 amplitude in a visual target detection task. We hypothesize that target detection time will be faster and possibly more accurate for those trials where ongoing alpha develops seamlessly into the P_1 as compared to not seamless trials. Seamlessness was determined on the basis of a single trial selection algorithm as described in the Material and methods section below. In addition, we manipulated temporal expectation by using fixed or varied inter-stimulus intervals (ISIs).

Material and methods

The data of a visual target detection task were used to analyze the relationship between ongoing alpha phase and the appearance of the P_1 component. Subjects had to respond as quickly as possible to a briefly exposed (80 ms) visual target stimulus (centered presentation). Two targets, consisting of the letter either ‘q’ or ‘p’ were used. Subjects responded with the index finger of their dominant hand by pressing a left response key to the target ‘q’ and a right response key to ‘p’. The reaction time (RT) was measured. Two conditions, a fixed and varied presentation condition were performed in that order. The fixed condition consisted of 4 blocks with 130 items each. Within these blocks, the ISI was kept constant at 500 ms for Block 1, 550 ms for Block 2, 700 ms for Block 3 and 750 ms for Block 4 (cf. Table 1). Blocks were randomized between subjects. The variation of the ISI between the blocks was used to increase demands on temporal attention. In the varied condition, a random distribution of the ISI-duration in the range of 500 to 750 ms was used with an average of about 500 trials per subjects (details see Table 2).

Subjects

A sample of 14 subjects, seven women and five men, 20 to 25 years of age ($M = 22.22$; $SD = 1.72$), participated in the experiment. Due to technical problems, the data of 2 subjects had to be removed from the fixed condition.

EEG recordings

The EEG was recorded by using a 64-channel BrainAmp amplifier (BrainProducts, Inc., Gilching, Germany). EEG-signals were online referenced against the nose and subsequently (off-line) re-referenced to digitally averaged ($[A1 + A2] / 2$) ear lobes. Band-pass filters were

Table 1
ISI's for the FIX and VAR condition. The length of the ISI for the VAR condition has been uniformly distributed in the range of 500–750 ms.

ISI	Block	Blank	Fixation +	ISI (blank screen)	p or q	qp
FIX	1	750 ms	250 ms	500 ms	80 ms	1000 ms
	2			550 ms		
	3			700 ms		
	4			750 ms		
VAR	5	750 ms	250 ms	500–750 ms	80 ms	1000 ms