

Alpha synchronization and anxiety: Implications for inhibition vs. alertness hypotheses

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Received 6 December 2004; received in revised form 8 February 2005; accepted 18 March 2005

Available online 14 June 2005

Abstract

Although there is much evidence that alpha oscillations are linked with processes of perception, attention and semantic memory, their functional significance remains uncertain. Synchronization in the alpha frequency range is taken to be a marker of cognitive inactivity, active inhibition of sensory information, or a means of inhibition of non-task relevant cortical areas. Here we propose an alternative interpretation which posits that higher alpha power during reference interval signifies higher readiness of alpha system to information processing. Predictions derived from the inhibition and alertness hypotheses were tested during presentation of acoustic stimuli (tone 1000 Hz) and neutral words to 30 males (18–25 years) with different levels of trait anxiety. On the whole, predictions derived from the inhibition theory were not confirmed and findings more corresponded to the alertness hypothesis. High-anxiety subjects showed higher alpha power during reference interval simultaneously with higher magnitude of event-related desynchronization and higher amplitude of phase-locked alpha responses. These findings are discussed in terms of functional significance of alpha band synchronization and desynchronization.

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Keywords: EEG; Alpha oscillations; Anxiety; Event-related desynchronization; Averaged evoked potential

1. Introduction

Some data indicate that alpha oscillations are enhanced in anxious individuals particularly in anxiogenic environment (Bell et al., 1998; Herrmann and Winterer, 1996; Knyazev et al., 2002, 2003, 2004a,b; Knyazev and Slobodskaya, 2003). This enhancement has been interpreted as a sign of higher readiness of alpha system for information processing (Knyazev and Slobodskaya, 2003). Prima facie, this interpretation seems dubious since enhanced alpha oscillations have long been considered as an attribute of relaxation. Indeed, starting from Berger's (1929) pioneering works, many studies have noted a task-related decrease in alpha power. This finding was so pervasive that alpha power has come to be considered as a reverse measure of activation. More recently this idea has been reconceptual-

ized to propose alpha as a mechanism for increasing signal to noise ratios within the cortex by means of inhibition of unnecessary or conflicting processes to the task in hand (Klimesch et al., 1999, 2000)—the greater the task demands, the more inhibition needed, the greater the synchronization. Klimesch's proposals are compatible with the notion of “surround inhibition” wherein active cortical areas, indexed by alpha desynchronization are surrounded by a “doughnut” of alpha synchronization or inhibition (Suffczynski et al., 2001; Pfurtscheller, 2003) in keeping with Crick's (1984) spotlight of attention hypothesis.

The idea of inhibitory function for alpha synchronization is appealing but it raises some doubts. First, it is not clear how the same mechanism might be linked with perceptual activation, as in the case of phase-locked evoked alpha oscillations (Basar, 1998, 1999), and perceptual inhibition (as proposed for event-related alpha synchronization, ERS). Next, if ERS served a function of selective attention (e.g. inhibition of non-task-relevant perception), one would expect that relatively small cortical area within a task-

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relevant zone would show ERD whereas larger cortical areas, which are not related to the task processing, would show ERS. That would correspond to the Crick's spotlight of attention hypothesis. The more focused is attention (e.g. in the beginning of an experiment) the more widespread ERS and more localized event-related desynchronization (ERD) should be observed. Actually the opposite applies. Alpha ERD is a much more common and widespread phenomenon than alpha ERS. It is usually more pronounced and widespread during first presentations of a signal or a task. It is stronger during more complex tasks compared to the relatively simple ones (Neubauer et al., 1999). All these observations are difficult to reconcile with the idea of lateral inhibition as a function of ERS.

Owing to extensive studies by Basar (1998, 1999) as well as other authors (Klimesch, 1999), a considerable body of knowledge has been accumulated indicating that depending on background activity, different reactions of EEG bands could be observed. According to the concept proposed by Basar (1998), the ongoing EEG determines (controls) evoked activity. This signifies that through the maintenance of higher or lower power of specific oscillations, brain could be prepared or predisposed to specific pattern of responses. Klimesch (1999) states that the reactivity in band power can be predicted from the amount of absolute power as measured during a resting state. Considering the reactivity of alpha band he notes that large alpha power is associated with a large amount of desynchronization during task performance. He concludes that the most reactive individuals would show in resting condition significantly more power in the alpha band.

It is not intuitively clear why a state of expectation of a perceptual event during the reference interval should be associated with inhibition of those same cortical areas, which later will be engaged in perception of this event. It is well known that inhibition is associated with diminished responsiveness. For example an inhibited (that is, hyperpolarized) neuron is not responsive to external stimuli. Contrary to that, above discussed evidences imply that alpha enhancement during inter-stimulus interval is associated with enhanced responsiveness. Therefore we suggest that in this case alpha synchronization should not be considered as "inhibition" of correspondent networks. On the contrary, it reflects active preparation of the alpha system to a demanding task.

Our interpretation is as follows. The EEG consists of the activity of an ensemble of generators producing rhythmic activity in several frequency ranges. These oscillators are active usually in a random way. By application of sensory stimulation these generators may be coupled and act together in a coherent way. This synchronization and enhancement of EEG activity gives rise to "evoked" or "induced rhythms" (Basar et al., 2000). Synchronization is the typical arousal reaction for delta, theta, high beta, and gamma rhythms. Desynchronization is mainly peculiar to alpha and lower beta but these rhythms also show

synchronization when evoking events are relatively simple for processing. If a task demands additional cortical structures and diverse processes to be involved, alpha oscillators disintegrate to smaller groups participating in different processes and this reveals itself in event-related desynchronization. The extent of alpha desynchronization should correlate with perceived complexity of a task or importance of a signal and reflects allocation of resources needed for its management. But in order to effectively process a demanding signal, the alpha system has to be prepared. That means that alpha oscillators should be disengaged from their current random activity and gathered into a united system ready to action. This reveals itself in anticipatory or preparatory alpha synchronization which is the best background for ERD. Research indicates that this is also the best condition for good performance. For example, a large upper alpha power in a reference interval preceding a task is related to both large suppression of upper alpha power during the task and good performance (Klimesch, 1999). Moreover, artificial enhancing of alpha power by means of repetitive transcranial magnetic stimulation at individual upper alpha frequency can enhance task performance and, concomitantly, the extent of task-related alpha desynchronization (Klimesch et al., 2003).

In the present study, we intended to check whether assumptions derived from the inhibition theory may explain changes of alpha power and reactivity during repetitive presentation of neutral words to subjects with different levels of trait anxiety. According to this theory, alpha synchronization is associated with inhibition of non-relevant cortical areas. The more attention to the stimuli, the more inhibition is needed. Therefore, one would expect that perception of acoustic stimuli should be associated with alpha ERD within central cortical regions, and alpha ERS within cortical areas not associated with acoustic perception (e.g., posterior regions). ERS should be more pronounced and widespread in the beginning of stimuli presentation and should diminish after repetitive presentation of the same stimuli due to extinction of attention. It also should be more evident in subjects with higher trait anxiety, since it is well established that these subjects are predisposed to enhanced attention to novel stimuli in unfamiliar environment (Gray, 1987).

Alternative interpretation posits that higher background alpha power signifies higher readiness of alpha system and should be associated with higher reactivity (that is, ERD). In the between-subject domain this implies that anxious individuals, tending to show more power of alpha oscillations in resting conditions (Knyazev et al., 2002, 2003, 2004a,b; Knyazev and Slobodskaya, 2003), would be more predisposed to react to external stimuli by alpha desynchronization. In the within-subject domain, we expected that ERD would be most pronounced within cortical area with highest alpha power (i.e. posterior region). Note that this is in sharp contrast with expectation derived from the inhibition theory, which predicts ERS in this region. Further,

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