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Review

Review of evoked and event-related delta responses in the human brain

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ABSTRACT

In the last decade, the brain's oscillatory responses have invaded the literature. The studies on delta (0.5–3.5 Hz) oscillatory responses in humans upon application of cognitive paradigms showed that delta oscillations are related to cognitive processes, mainly in decision making and attentional processes.

The present manuscript comprehensively reviews the studies on delta oscillatory responses upon cognitive stimulation in healthy subjects and in different pathologies, namely Alzheimer's disease, Mild Cognitive Impairment (MCI), bipolar disorder, schizophrenia and alcoholism. Further delta oscillatory response upon presentation of faces, facial expressions, and affective pictures are reviewed. The relationship between pre-stimulus delta activity and post-stimulus evoked and event-related responses and/or oscillations is discussed. Cross-frequency couplings of delta oscillations with higher frequency windows are also included in the review.

The conclusion of this review includes several important remarks, including that delta oscillatory responses are involved in cognitive and emotional processes. A decrease of delta oscillatory responses could be a general electrophysiological marker for cognitive dysfunction (Alzheimer's disease, MCI, bipolar disorder, schizophrenia and alcoholism). The pre-stimulus activity (phase or amplitude changes in delta activity) has an effect on post-stimulus EEG responses.

1. Introduction

The superposition of evoked and induced oscillations in different frequency windows gives rise to Evoked Potentials (EPs) and/or Event-Related Potentials (Başar, 1980, 1998, 1999). In his book *EEG-Brain Dynamics*, Başar (1980) described the relationship between spontaneous EEG and the characteristics of evoked potentials in the frequency domain and in the time domain. In the frequency domain, it was commented that spontaneous EEG and the EPs have common frequency bands, and, upon stimulation, spectral regularization of the EEG occurs. In the time domain, oscillatory responses could have damped oscillatory character; amplitude enhancement could occur in most of the response components. Time locking among responses to successive stimuli gives rise to induced activity. The correlation between the response and the EEG prior to stimulus was also described. After thirty-four years of research in the area of brain oscillatory responses, all the properties of the brain oscillatory responses mentioned above have been supported by many researchers working in this area (Lakatos et al., 2008, 2013; Besle et al., 2011; Cravo et al., 2013; Gomez-Ramirez et al., 2011; Henry and Obleser, 2012; Kösem et al., 2014; Stefanics et al., 2010; Jones et al., 2006; Bernat et al., 2007; Ishii et al., 2009).

Delta oscillatory responses are defined as EEG oscillatory responses in the 0.5–3.5 Hz frequency range. In the human brain, Başar and Stampfer (1985) and Stampfer and Başar (1985) were among the first researchers who demonstrated the importance of delta responses in cognitive processes. Currently, publications support the view of these authors that delta responses are involved in cognitive processes, mainly in decision-making and attentional processes.

To our knowledge, there are two previous reviews on delta oscillations (Harmony, 2013; Knyazev, 2012). Knyazev (2012) reviewed delta oscillations with the thesis that delta oscillation manifests the most ancient oscillatory mode in comparison to higher frequencies. This review is different from the other two in that we mainly focus on the delta oscillatory responses rather than spontaneous EEG delta activity. Our review includes studies on event-related delta responses upon cognitive and emotional paradigms. We primarily focus on the human Evoked and/or Event-Related delta responses during sensory, cognitive, or emotional processes. We further will emphasize the role of delta responses as a candidate general electrophysiological marker in cognitive dysfunctions as Alzheimer's disease, mild cognitive impairment, bipolar disorder, schizophrenia, and alcoholism. Cross-frequency couplings of delta oscillations with higher frequency windows and the relation of pre-stimulus delta activity with post-stimulus EEG responses will be also discussed.

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2. Generators of delta activity

Research has shown several generators of delta oscillations in human brain. Long-lasting hyperpolarizations generated by pyramidal neurons yield EEG delta oscillations (Steriade, 1993; Steriade and Buzsaki, 1990; Steriade et al., 1990). Glial cells have also been reported to produce slow oscillations (Amzica, 2002; Amzica and Steriade, 2000). Two intrinsic currents of thalamocortical cells generate delta oscillations (Steriade, 1993). Delta oscillations have also been recorded from nucleus accumbens (Leung and Yim, 1993), dopaminergic neurons in the ventral tegmental area (Grace, 1995), ventral pallidum (Lavin and Grace, 1996), and brain stem (Lambertz and Langhorst, 1998).

3. Analysis of delta oscillatory responses

There are several types of oscillatory activity in the brain

1) Spontaneous EEG oscillations are those recorded without any external physical stimulation.
2) Evoked oscillations are evoked upon application of a pure sensory stimulation, i.e. upon any visual or auditory stimulation.
3) Event-related oscillations are elicited by application of a stimulation containing a task or strategy, i.e. oddball P300 response.

Table 1 summarizes some of the system theory methods used to analyze the spontaneous EEG, Evoked, and Event-Related oscillations. As we also mentioned in our recent review (Güntekin and Başar, 2014), there are several mathematical tools to analyze the evoked/event-related spectra. One of the most commonly used is the Fast Fourier Transform (FFT). First, in order to perform Fourier analysis of brain responses, an averaging procedure is applied to the data; following artifact rejection, selective averaging is performed. The averaged potentials (EP and/or ERP) are then analyzed via FFT and, according to the cut-off frequencies of evoked power spectra, digital filtering is applied to EPs or ERPs (e.g. for delta, 0.5–3.5 Hz; for theta, 4–7 Hz; for alpha, 8–13 Hz; for beta, 14–30 Hz; and for gamma, 28–48 Hz filters are applied). A grand average is also applied by performing averaging across subjects. It is possible to conduct statistical analysis of evoked/event-related power measures and to analyze the peak-to-peak amplitudes of filtered oscillatory responses (Başar, 1998, 1999).

Table 1
The ensemble of systems theory methods.

The ensemble of systems theory methods
a) Analysis of spontaneous EEG
• Power spectral density of the spontaneous EEG
• Spontaneous EEG coherence
• Cross frequency analysis (relation between different frequency windows: phase to phase, phase to amplitude, amplitude to amplitude couplings)
b) Analysis of evoked oscillations (elicited by simple light, tone signal, etc.)
• *Evoked spectra* (FFT or similar mathematical analysis of the sensory-evoked potential)
• Digital filtering (digital filtering of the sensory-evoked potential in 0.5–3.5 Hz for delta oscillatory responses)
• Phase-locking
• Evoked coherence between two electrode pairs
• Cross frequency analysis (relation between different frequency windows: phase to phase, phase to amplitude, amplitude to amplitude couplings)
c) Analysis of event-related oscillations (elicited by an event, for example target or non-target signal during an oddball paradigm)
• Event-related spectra (FFT or similar mathematical analysis of an event-related potential)
• Digital filtering (digital filtering of the sensory-evoked potential in 0.5–3.5 Hz for delta oscillatory responses)
• Phase-locking
• Event-related coherence between two electrode pairs
• Cross frequency analysis (relation between different frequency windows: phase to phase, phase to amplitude, amplitude to amplitude couplings)

When FFT or any other mathematical tool is applied to EPs or ERPs, the phase-locked activity is primarily represented in the transform. However, oscillatory responses could instead include time-locked activity, which is termed induced activity (Başar, 1998, 1999). In order to see the induced activity, it is possible to apply FFT or any other mathematical tool (e.g. wavelet transform) to the single epochs, and then the evoked and induced activities (total power) are analyzed by averaging the FFTs of these epochs. In order to obtain only the induced power, evoked power is excluded from the total power (Herrmann et al., 2004).

Event-related phase consistency across trials is an important method allowing researchers to see how phase information varies between trials. Kolev et al. (1998) used single-sweep wave identification (SSWI) histograms to analyze phase-locking. Tallon-Baudry et al. (1996) defined a method called phase-locking factor, and Delorme and Makeig (2004) called this method inter-trial phase coherence (ITPC). Lachaux et al. (1999) defined a method called phase-locking statistics, in which responses to repeated stimuli were used to identify latencies at which the phase difference between the signals varies little across trials and between two electrode sites.

The analysis of spontaneous EEG coherence, evoked coherence and event-related coherence between two electrode pairs is an important tool to understand functional connectivity between two different electrode pairs (Bendat and Piersol, 1967; Lopes da Silva et al., 1980; Petsche and Etlinger, 1998; Rappelsberger et al., 1982). Successful use of Evoked and/or Event-Related coherences has been reported previously for healthy subjects (Güntekin and Başar, 2010; Qassim et al., 2013), Alzheimer's patients (Başar et al., 2010; Güntekin et al., 2008), and bipolar disorder patients (Özerdem et al., 2010, 2011) upon application of the oddball paradigm.

4. Relation between P300 and delta oscillatory responses

In neuroscience, references to the target response during the oddball strategy are often associated with the delta response. This is only partially the case. The delta response is the damped oscillatory response, which is obtained following digital filtering in the frequency window of 0.5–3.5 Hz (black curve in Fig. 1). However, the target response also contains other oscillatory responses in theta, alpha, beta and gamma frequency ranges (Başar-Eroğlu and Başar, 1991; Başar-Eroğlu et al., 1991, 1993, 2001; Demiralp et al., 1999, 2001; Güntekin et al., 2013; Karakaş et al., 2000; Kolev et al., 1997; Sakowitz et al., 2001; Schürmann et al., 1997; Spencer and Polich, 1999; Öniz and Başar, 2009; Yordanova et al., 2000). Delta response, which is the most ample signal with a negative peak around 200 ms and positive peak around 400 ms, is superimposed with the theta response from which the second oscillation coincides with the delta response. Therefore, the unfiltered P300 response shows a sharp positive peak around 400 ms following the target stimuli. Due to this analysis, delta response gains importance in all studies in which a cognitive load is presented. This cognitive load, in turn, is correlated with attention, perception, learning, and memory. Further, with hearing and visual threshold signals, the only remaining component is the delta response, which allows assigning a perceptual decision to the delta response (Parnefjord and Başar, 1999).

We emphasize the analytic description in Fig. 1 because, in the present review, it will be shown that all types of cognitive deficits are accompanied by a reduction of the delta response. Accordingly, the description of the delta response gains high importance in all types of impairments related to cognitive deficits. The analysis of oddball experiments should indicate the interplay between delta and theta responses, as well as the alpha prolongation for the achievement of a cognitive process. However, in order to present an understandable and transparent interpretation of the P300 process, the consideration of the delta response alone highly facilitates the preliminary steps in electrophysiological understanding of cognitive processes.

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