Neuroscience and Biobehavioral Reviews 32 (2008) 1001–1013

Contents lists available at ScienceDirect

Neuroscience and Biobehavioral Reviews

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

Review

What does phase information of oscillatory brain activity tell us about cognitive processes?

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ARTICLE INFO

Article history:
Received 6 September 2007
Received in revised form 4 March 2008
Accepted 29 March 2008

Keywords:
Alpha rhythm
Attention
Coherence
Connectivity
Electroencephalography (EEG)
Gamma rhythm
Memory
Phase-locking
Theta rhythm

ABSTRACT

The electroencephalogram (EEG) bears the possibility to investigate oscillatory processes in the human brain. In the animal brain it has been shown that the phase of cortical oscillations is related to the exact timing of neural activity. The potential role of oscillatory phase and phase synchronization for the explanation of cortical information processing has been largely underestimated in the human EEG until now. Here it is argued that EEG phase (synchronization) reflects the exact timing of communication between distant but functionally related neural populations, the exchange of information between global and local neuronal networks, and the sequential temporal activity of neural processes in response to incoming sensory stimuli. Three different kinds of phase synchronization are discussed: (i) phase coupling between brain sites, (ii) phase synchronization across frequencies, and (iii) phase-locking to external events. In this review recent work is presented demonstrating that EEG phase synchronization provides valuable information about the neural correlates of various cognitive processes, and that it leads to a better understanding of how memory and attention processes are interrelated.

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doi:10.1016/j.neubiorev.2008.03.014

1. Introduction

1.1. Electroencephalography (EEG): a window into the human brain

For 80 years by now EEG has been used to record electrical activity from the human brain (Berger, 1929). It is a popular method to acquire neural signals in a non-invasive manner. Electrodes are placed on the scalp and the so recorded electrical fields are then amplified by a factor of approximately 1000.

The signal that is acquired by the EEG is comparable to the local field potential in cortex, but on a much larger spatial scale. This means that the sum activity of many millions of neurons generates the EEG. However, the recorded activity comes not from action potentials of cortical neurons but rather their dendritic activity (excitatory and inhibitory post-synaptic potentials EPSP/IPSP). So, what we see in the human EEG is the synchronous excitatory and/or inhibitory input into a large population of nerve cells. With EEG it is possible to get a glimpse of neural activity from the whole cortex. This makes EEG a very potent tool to study the interaction between brain areas and different cortical networks. Although spatially very imprecise (spatial resolution of scalp EEG is in the range of several centimeters), EEG provides excellent temporal resolution in the range of milliseconds. This is a big advantage over other modern neuroimaging tools such as functional magnetic resonance imaging (fMRI) or positron emission tomography (PET), as EEG does not rely on the hemodynamic response but records neural activity in real time. This provides also the possibility to analyze oscillatory brain activity, which will be a main focus in this review.

1.2. Oscillatory brain activity

Already Berger (1929) recognized that the electric activity of the human brain exhibits certain rhythmicity. He was the first who reported high amplitude oscillations around 10 Hz during a resting condition in which the subject had his/her eyes closed. He termed this activity 'alpha rhythm'. When the subject opened his/her eyes this 10 Hz alpha activity vanished and much faster rhythmic activity with lower amplitudes became dominant. He called this pattern 'beta rhythm'. Later, brain oscillations that are not easily visible in the healthy human (awake) resting EEG were labeled: 'Delta' refers to a frequency range between 0 and 4 Hz, 'theta' represents a rhythm between 4 and 8 Hz and 'gamma' oscillations describe activity above 30 Hz.

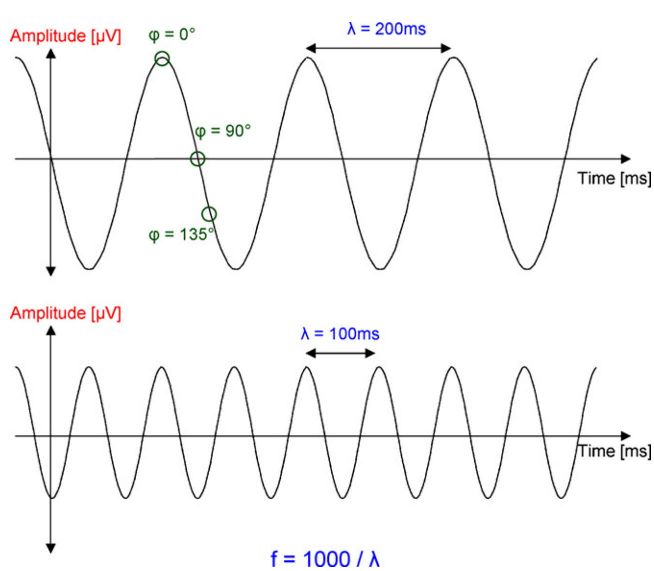

Fig. 1. Example of two periodic signals with different frequency and amplitude. In the upper panel the instantaneous phase of the cosine wave at three points in the time series are exemplified.

Any oscillation can be described by various parameters. These are: (i) the oscillation's frequency, (ii) its amplitude and (iii) its instantaneous phase. In Fig. 1 two examples of periodic signals are shown. The upper one has slower frequency ($f = 1000/200 = 5$ Hz) than the second one ($f = 1000/100 = 10$ Hz). Moreover, the second signal shows smaller amplitude than the upper one. In the upper panel the instantaneous phase angle of this cosine wave is given for three time points. In the EEG, all these parameters can bear important information. It will be discussed later how these parameters of oscillatory brain activity contribute to a better understanding of the human mind.

Given the idea that brain circuits of different size show different resonance properties one should expect that brain rhythms of different frequency can help dissociating specific brain networks (Von Stein and Sarnthein, 2000). This is underpinned by the fact that the classical EEG brain rhythms show different neural generators and also different functionality, as will be demonstrated in the following part.

1.2.1. Delta

Oscillations between 0 and 4 Hz are classically termed delta. Following Steriade (1999) oscillations below 4 Hz are generated by neocortical and thalamo-cortical networks. In terms of its functions in the brain, delta is important for large-scale cortical integration (Bruns and Eckhorn, 2004) and for attentional and syntactic language processes (Devrim et al., 1999; Schürmann et al., 2001; Roehm et al., 2004).

1.2.2. Theta

Theta oscillations can be found in the human cortex and the hippocampus (e.g., Kahana et al., 2001). A whole network of theta pacemakers is discussed (for an overview see O'Keefe and Nadel, 1978; Steriade, 1999) including the medial and lateral septum, hypothalamus, the hippocampus, the reticular-formation and further brain-stem structures. There is also the hypothesis that it is similarly generated as alpha oscillations, namely by thalamic nuclei (Hughes et al., 2004) and thalamo-cortical loops (Talk et al., 1999). Theta oscillations seem to be important for a variety of cognitive functions. For instance, in rats hippocampal theta, and its phase in particular, codes locations in space by influencing the temporal firing pattern of place cells (for reviews see O'Keefe and Nadel, 1978; Redish, 1999). Kahana et al. (1999) provided evidence that dominant theta activity can also be found in the human hippocampus. And it was shown that hippocampal and cortical theta activity or rhinal-hippocampal interplay was associated with virtual navigation (Kahana et al., 1999), declarative memory processes (Fell et al., 2003), successful memory encoding (Sederberg et al., 2003; Klimesch et al., 1996), the amount of information held in memory (Mecklinger et al., 1992; Tesche and Karhu, 2000; Klimesch et al., 1999; Jensen and Tesche, 2002) and episodic memory processing (e.g., Klimesch et al., 2001a,b).

1.2.3. Alpha

Inhibitory thalamic interconnection and thalamo-cortical feedback-loops are discussed to result in oscillatory activity between 8 and 13 Hz as are cortico-cortical networks (Lopes da Silva et al., 1980; Steriade, 1999; Nunez, 2000; Nunez et al., 2001). The functional relevance of these so-called alpha oscillations is very widespread. There is strong evidence that alpha amplitudes are related to the level of cortical activation. A strong alpha activity is associated with cortical and behavioral deactivation or inhibition (e.g., Klimesch et al., 1999, 2007a; Ray and Cole, 1985; Cooper et al., 2006; Hummel et al., 2002; Thut et al., 2006; Rihs et al., 2007;