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Review

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

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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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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.

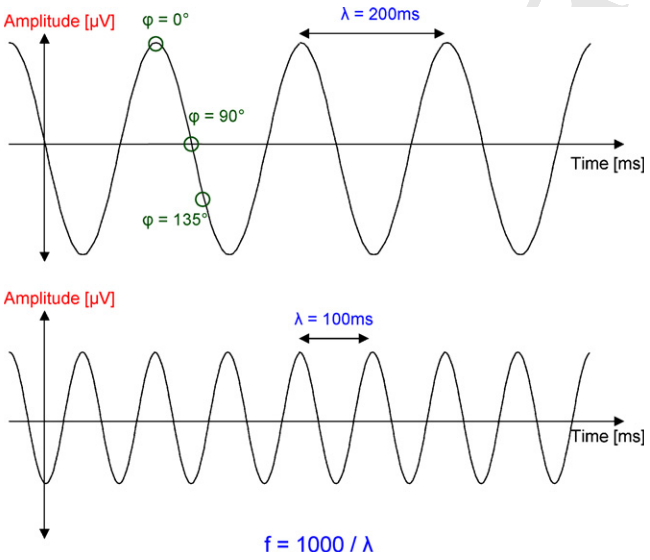

Fig. 1. Example of two periodic signals with different frequency and amplitude. In the upper panel the instantaneous phase of the cosine wave at three points in the time series are exemplified.

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., 2004). 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; Worden et al., 2000; Jensen et al., 2002). But it is also involved in

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highly specific perceptual (Ergenoglu et al., 2004; Hanslmayr et al., 2005; Thut et al., 2006), attentional (Von Stein et al., 2000; Worden et al., 2000; Sauseng et al., 2005c; Thut et al., 2006; Rihs et al., 2007) and memory processes (for reviews see Klimesch, 1997, 1999; Klimesch et al., 2005).

1.2.4. *Beta*

It has been emphasized that beta oscillations are cortically generated (e.g., Salenius and Hari, 2003), due to their local strictness. This is in contrast to Gross et al. (2004) who demonstrated widespread cortical beta networks in humans. From a functional perspective beta oscillations have mainly been associated with motor activity. During movements primary motor cortices exhibit a pronounced decrease of beta amplitudes whereas there occurs a strong beta power rebound when movements are stopped (see Neuper and Pfurtscheller, 2001). But beta has also been suggested to play an important role during attention (Bekisz and Wróbel, 2003; Gross et al., 2004; Wróbel et al., 2007) or higher cognitive functions (Razumnikova, 2004).

1.2.5. *Gamma*

There is large agreement that gamma oscillations (30–80 Hz) are cortically generated (see Steriade, 1999). It is emphasized that gamma oscillations arise from intrinsic membrane properties of interneurons or from neocortical excitatory-inhibitory circuits (Llinás et al., 1991; Gray et al., 1990). Since the pioneering work on the cat visual cortex by Gray, Singer and co-workers in the 1980 s gamma oscillations are well investigated and associated with visual awareness (Gray et al., 1989; for review see Engel and Singer, 2001). Synchronization phenomena of this brain rhythm were related to binding of information. More recently, effects at human gamma frequency were also reported for the encoding, retention and retrieval of information independent of sensory modality (e.g., Tallon-Baudry and Bertrand, 1999; Herrmann et al., 2004; Sederberg et al., 2003; Kaiser and Lutzenberger, 2005; Kaiser et al., 2006; Leiberg et al., 2006; for review see Kahana, 2006). Although it has also been discussed that gamma binds large-scale brain networks (Rodriguez et al., 1999; for a review see Varela et al., 2001) this view has been challenged more recently. Instead it is more likely that gamma oscillation reflect strictly local activity (Von Stein and Sarnthein, 2000; Bruns and Eckhorn, 2004). However, it should be mentioned that recording gamma activity in the human EEG is difficult due to the very small amplitude of gamma oscillations and the similarity in terms of its frequency characteristics with electrical muscle activity that is accidentally also recorded by the EEG.

For most of the above described frequency bands reactivity in response to cognitive processes was reported in terms of amplitude modulations. Slow frequency bands (delta and theta) as well as very fast oscillations (gamma) tend to increase in amplitude during cognitive effort whereas alpha and beta rhythm usually show an amplitude reduction during active cognitive processing (see Basar et al., 2001; Basar-Eroglu et al., 1996 for reviews). Measures for the reactivity of frequency bands were developed to describe event-related amplitude in- and decrease (e.g., Pfurtscheller and Aranibar, 1977; Salmelin and Hari, 1994). Using these methods it was shown that amplitude variations very selectively indicated cortical activation/deactivation in various sensory and cognitive modalities (see, e.g., Klimesch, 1999; Neuper and Pfurtscheller, 2001; Neuper et al., 2006; Hummel and Gerloff, 2006). These event-related or task-related changes have a temporal preciseness of a few hundred milliseconds (Woertz et al., 2004). Compared to the hemodynamic response this is fast. However, neuronal communication in the brain relies on dramatically faster processes (in the range of only a few milliseconds; see, i.e. Buzsaki and Draguhn, 2004; Dragoi and Buzsaki, 2006; Siapas et al., 2005). Therefore, EEG amplitude seems not to be very informative about fast changes in task-related neural processing but rather reflects sustained activation and deactivation patterns of larger cortical patches. It has been reported that the instantaneous phase of (primate) brain oscillations is associated with particular neuronal firing patterns and high temporal preciseness of neural activity (Buzsaki and Draguhn, 2004; Hirase et al., 1999; Harris et al., 2002). It was also shown that the instantaneous phase of hippocampal theta activity (in the rat) directly influences the temporal firing pattern of place cells CA1 neurons (for reviews see O'Keefe and Nadel, 1978; Redish, 1999). Thus, also in the human brain, phase information from EEG might tell us much more about the neural activity related to cognitive processes *per se* than do amplitude estimates. However, compared to the large body of research regarding amplitude modulations in the EEG, human studies in cognitive neuroscience using phase information from cortical oscillatory activity still are under-represented. As outlined in the following, recently, new methods measuring different aspects of phase synchronization in the human brain have been applied to the EEG to more precisely describe how memory and attentional processes are neuronally implemented.

2. Phase synchronization in the brain

Neurons in the human brain are to a very large extent interconnected. Therefore, one can see the whole brain as a huge network consisting of millions of sub-networks ranging from micro-level to large-scale connections (see Varela et al., 2001 for review). It is widely accepted that information is stored in neural networks and human behavior arises from extremely complex communication between neurons in these networks and also between separate networks or assemblies (see Fuster, 1997; Varela et al., 2001). Actually, in macaques it was even shown, that the function of neighboring single neurons can be completely different depending on which other cells they are coupled with (Fuster, 1998; Quintana and Fuster, 1999). This is supported by Richmond et al. (1997), who also demonstrated that neighboring neurons in V1 and inferior temporal cortex show maximal variance so that within cortical layers information loss can be minimized.

As already mentioned above, the EEG can only record neural activity when there is simultaneous dendritic activity in a large population of neurons, or more precisely if there is very high synchrony in the cortex underlying the electrode. If we consider that the spatial resolution of scalp EEG is in the range of some centimeters it comes evident that with this method it is not possible to investigate network properties on a micro-level, such as the synchrony of a few connected single cells. Instead, with EEG we can only make inferences about synchronicity on a large scale. So, if we speak of 'local' activity later on, activity within a cortical batch of some centimeters is meant. 'Global', 'large-scale' or 'long-range' on the other hand will refer to activity covering distances between cortical lobes or even hemispheres. Therefore, below the term 'synchronization' will only be used for phenomena on a local or global scale but not on a micro-level which cannot be resolved with the scalp EEG.

The following section will focus on three different kinds of phase synchronization on a local and global level: (i) phase coupling over distance, (ii) phase coupling between frequencies, and (iii) phase-locking (phase resetting) in response to onset of sensory stimuli.

If two cortical areas show very similar brain activity, and this brain activity is related to each other in a fixed manner, one can deduce from it that the two brain areas are somehow functionally

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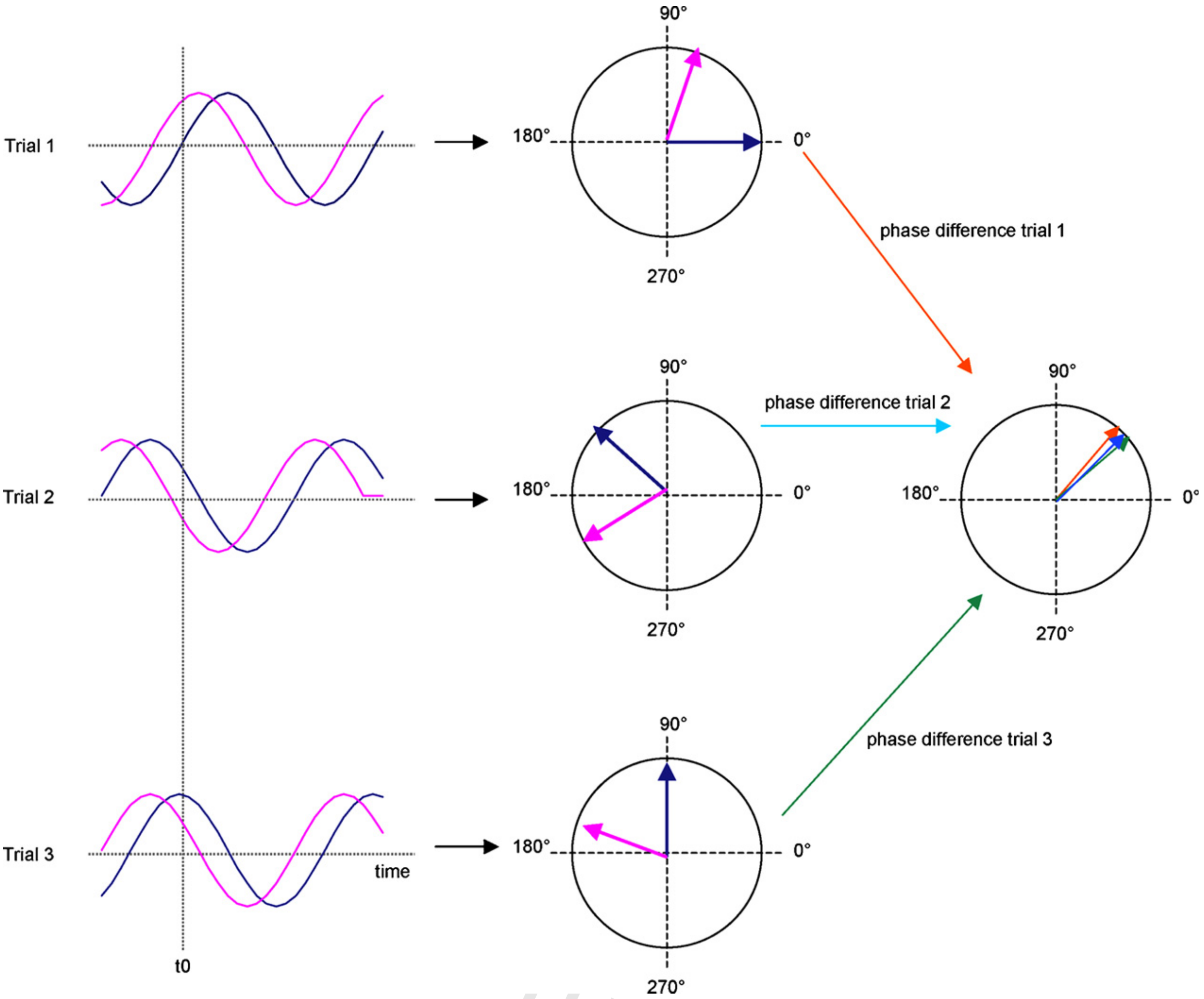

Fig. 2. The signals from two electrodes (pink and blue) from three single trials are depicted. At time *t*0 the instantaneous phase angle of each of the signals is estimated and the phase difference between the pink and the blue electrode is calculated for each trial. It becomes obvious then that independent of absolute phase angle at *t*0 the lag between the two electrodes is always the same, and thus, phase coherence will be high. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

related, as they do the same thing at the same time. Phase coherence is then a measure to quantify the similarity between two signals from the brain. In Fig. 2 oscillatory activity from two electrode sites is schematically depicted. In all three trials the difference of instantaneous phase angles at time *t*0 is very similar—independent of the absolute phase angles of these oscillations. When the phase differences from all single trials are then averaged high phase coherence values will be the result. So if the phase angles of an oscillation recorded at EEG-electrodes A and B show the same lag in every single trial the similarity and thus the phase coherence, will be very high for these two sites. One can thus conclude that these two brain sites are somehow functionally related to each other and are involved in task-relevant processes.

Another kind of EEG synchronization is phase coupling across different frequencies. One can assume that networks of different size oscillate at different frequency due to their different resonance frequency. Thus, there must be some synchronization of the two underlying network oscillations of different frequency to exchange information. To quantify this, methods such as bi-coherence or cross-frequency phase synchronization indices have been developed (Schack and Weiss, 2005; Schack et al., 2002; Palva et al., 2005). In the EEG you should obtain high cross-frequency phase synchronization if, although the two oscillations have different frequency, their phase lag at a certain time point is always constant, independent of absolute instantaneous phase angles.

A third type of phase synchronization that will be addressed later is phase-locking to onset of an external stimulus. The underlying idea is that after presentation of a sensory stimulus to the brain one usually obtains a so-called event-related potential (ERP). It has been discussed that these ERPs are generated by a phase resetting of brain oscillations (see, e.g., Sayers et al., 1974; Basar, 1999a,b). This means that in each single trial in response to an external stimulus ongoing phase of a certain frequency is reset. When the single trials are averaged, then the activity before the reset (which over trials is random in phase) should approach zero, whereas after the phase reset an event-related brain response should be the result. Therefore, this so-called phase-locking to stimulus onset indicates the involvement of certain frequencies in the strict timing of cognitive activity related to stimulus processing in order to established sensitive time windows and a temporal order for information processing (Klimesch et al., 2006).

In this section, the functional meaning of these three mechanisms will be discussed. It will be shown that brain synchronization phenomena reflect highly specific neural activity that provides information about different cognitive functions which cannot be derived from other methods and brain activation measures.

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Table 1
Q5 Frequency specific effects of interregional phase coupling on cognitive functions

Cognitive function	Theta	Alpha	Beta	Gamma
Multisensory integration		Classen et al. (1998), Hummel and Gerloff (2005)		Miltner et al. (1999)
Complex motor behavior		Gerloff et al. (1998), Andres and Gerloff (1999), Andres et al. (1999)		
Conscious visual perception		Kopp et al. (2000), Mima et al. (2001)		Rodriguez et al. (1999)
Visual attention		Sauseng et al. (2005b)	Gross et al. (2004)	
Declarative memory	Sarnthein et al. (1998), Sauseng et al. (2004)	Weiss and Rappelsberger (2000)		
Executive functions of WM	Sauseng et al. (2005a, 2006, 2007a)	Sauseng et al. (2005c)		

2.1. Phase coupling over distance: coherence between brain sites

In recent years there has been large agreement about the assumption that most cognitive processes do not solely rely on brain activity of small isolated brain areas but on activity of widespread networks of brain structures. Following the principle ‘what is wired together, fires together’ it is assumed that distant and task-relevant brain sites will become co-activated during specific cognitive demands. Coherence between EEG electrode sites has been used as measure for such synchronous co-activation (for methodological details see Nunez et al., 1997, 1999; or Rappelsberger, 1998). In cognitive neuroscience this method has been applied in research about motor functions, visual perception, multisensory integration, attention and memory.

Coherent oscillatory brain activity in distributed cortical networks has been demonstrated to play an important role for human behavior (the relevance of interregional phase coupling at certain frequency ranges for several cognitive functions is summarized in Table 1). For instance, it was shown that the integration between visual and haptic information is associated with the coupling of visual and somato-sensory cortices within the alpha, beta and gamma frequency band (Classen et al., 1998; Miltner et al., 1999; Hummel and Gerloff, 2005). Hummel and Gerloff (2005) could even demonstrate that performance in a multisensory integration task can be predicted by coherence between visual and somato-sensory cortex in the EEG alpha band during task execution. Also for motor behavior phase-coherent cortical network activity is considered essential. As an example Gerloff et al. (1998) reported strong connectivity in a distributed alpha network including primary motor and premotor cortex, supplementary motor area, prefrontal and parietal brain sites in both hemispheres during the execution of simple finger movements. Moreover, such a distributed synchronous cortical network was found relevant during bimanual motor tasks and the learning of sequential finger movements (Andres et al., 1999; Andres and Gerloff, 1999).

Conscious visual perception was also observed to be related to distributed network activity. Widespread coherence in the gamma and alpha frequency bands were reported to increase during conscious perception of visual scenes compared to unpercepted stimuli (Rodriguez et al., 1999; Klopp et al., 2000; Mima et al., 2001). In advance, attentional and working memory functions in part are correlated with phase-coupling of prefrontal and posterior brain areas. Gross et al. (2004) have shown that fronto-(parieto)temporal beta coherence is relevant for the processing of stimuli in working memory. They used rapid serial visual presentation tasks in which 2 targets were shown within a string of shortly presented letters. In such experimental designs usually a target is not detected (processed in working memory) when it is preceded by a first target roughly 300 ms before (this effect is known as attentional blink; Shapiro et al., 1997). As was demonstrated by Gross and co-workers, the second target is only processed when there is increased phase synchronization between prefrontal and parieto-temporal brain regions in the beta frequency band. Other brain activation measures, such as EEG amplitude, could not dissociate between processed and unperceived targets. But also in the theta and the alpha frequency band coherent fronto-parietal activity was found relevant for memory processes. During the transient storage of visuo-spatial and verbal material increased theta coherence between prefrontal and temporal and parietal sites was reported (Sarnthein et al., 1998). Data from Weiss and Rappelsberger (2000) on the other hand even indicate that the amount of long-range alpha coherence during the encoding of words predicts later retrieval of this stimulus material. So, one can assume that large-scale phase coherence, in particular, represents a highly specific correlate of human memory processes.

In an experiment on memory encoding and retrieval of visual information Sauseng et al. (2004) found a similar fronto-temporoparietal network active like the one described by Sarnthein et al. (1998). During both tasks, encoding and retrieval, prefrontal electrode sites were coupled with temporoparietal brain areas. In the task run by Sauseng et al. (2004) encoding required only the processing of visual information whereas during retrieval verbal and visual information had to be recalled at the same time. Interestingly, during encoding prefrontal brain sites were exclusively coupled with right posterior electrode sites whereas during retrieval we found significant connectivity between anterior and bilateral temporoparietal sites. This shows that theta phase coupling was strictly dependent on the modality (visual vs. verbal) of the encoded or retrieved material. In advance, using a cross-correlation approach, the direction of information flow between prefrontal and posterior sites had been determined. During encoding as well as during retrieval the frontal cortex was leading posterior cortical areas by approximately 30 ms on average. This suggests a monitoring function of the prefrontal cortex during the encoding of information and during access to working memory, whereas posterior brain areas seem more likely to reflect storage sites. Therefore, it was assumed that fronto-parietal theta coupling is relevant for the executive control of working memory processes. This was further investigated in a study by Sauseng et al. (2005a). In a visual working memory task epochs in which information merely had to be recalled from memory were compared with such time segments in which internally represented visual information had to be mentally manipulated. Thus, in the second condition (manipulation) there was larger central executive demand. Compared to sole retrieval there was stronger long-range connectivity at theta frequency between frontal and parietal/occipital sites during the manipulation condition. Anterior and posterior theta short-range coupling did not differentiate between the conditions with different executive demand, nor did theta amplitude. However, as retrieval and manipulations could not be compared concerning task-difficulty in the study by Sauseng et al. (2005a) a task switching experiment was run (Sauseng et al., 2006). In this research it was possible to compare trials in which

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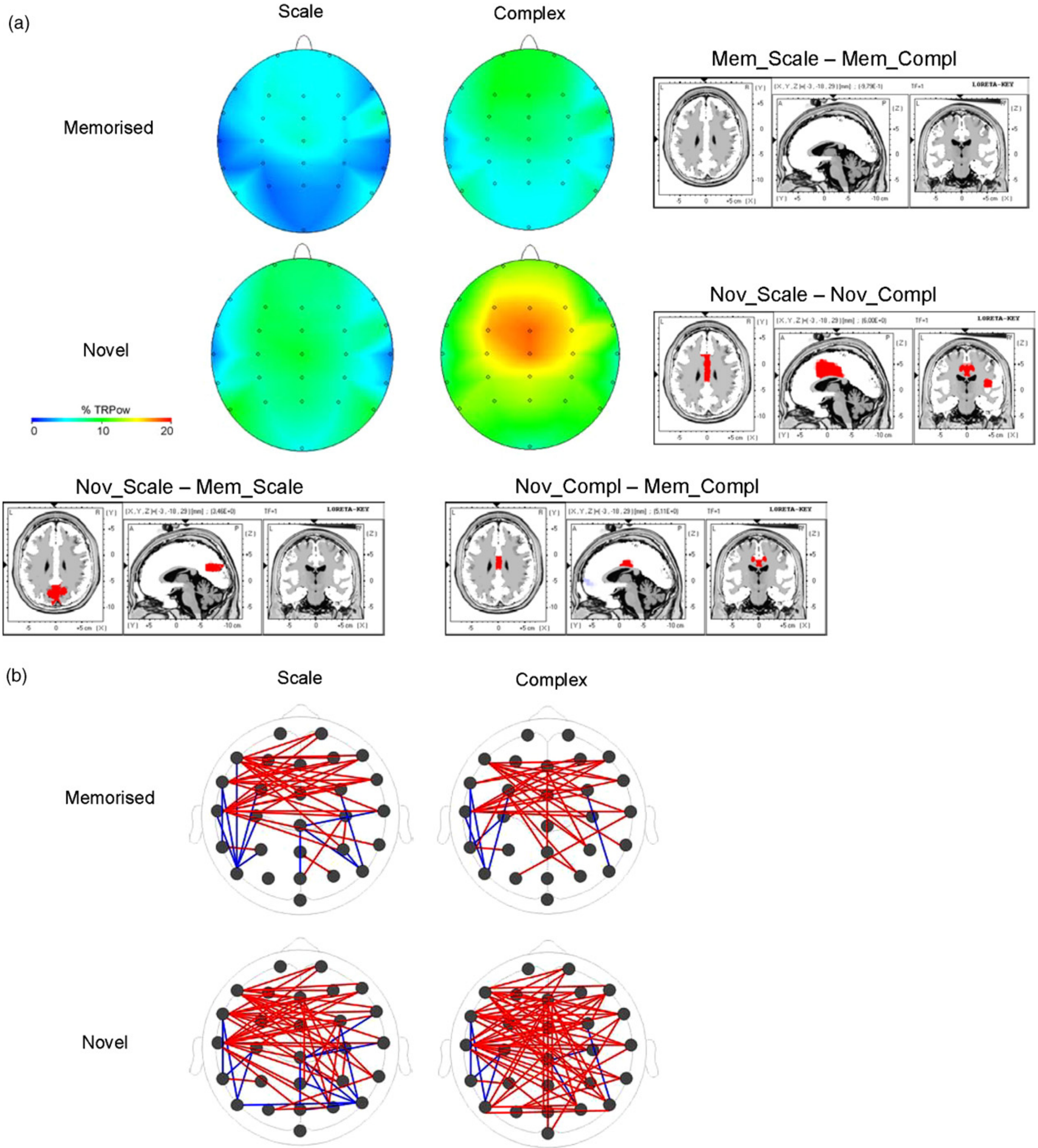

Fig. 3. During the execution of easy (scale) and more demanding (complex) finger sequences which were either novel or well-trained there was frontal midline theta activity only found in the most demanding condition (Sauseng et al., 2007a). Frontal midline theta power could not dissociate between learned and novel sequences. Execution of novel complex sequences was the only condition that showed significantly more theta activity in the anterior cingulate gyrus and cingulate motor area (localized using a current source density estimating approach) compared to all other conditions (a). Long-range theta phase coupling, on the other hand, was increased during execution of novel sequences, independent of task complexity (b), this shows that phase information responded to memory processes that were not dissociable with EEG power estimates. (Figure modified from Sauseng et al., 2007a.)

subjects had to switch from one simple task to another and therefore had to refine their task set (switch trials) with trials in which stimuli had to be processed following the same task set as in the preceding trial (stay trials). Therefore, the central executive of working memory was more activated in switch than in stay trials, with other variables such as task-difficulty or visual stimulus properties held constant. Well in line with the results of Sauseng et al. (2004, 2005a), in switch trials a distributed long-range fronto-parietal theta network was more activated than in stay trials (Sauseng et al., 2006). EEG theta amplitude in contrast did not differentiate between switch and stay trials. In the experiment part of the trials were highly predictable (whether there would be a task switch or not) and part of the trials were not predictable. Switch and stay trials were thus separated regarding their predictability and it was found that fronto-parietal theta coherence did purely differentiate between switch and stay but independently of predictability. A low alpha frequency band on the other hand responded to predictability. This indicates that long-range phase

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synchrony at theta frequency is primarily involved in executive and monitoring functions of working memory, independent of task-difficulty, predictability or attention and perception.

In a recent study (Sauseng et al., 2007a) this knowledge was used to separate effects of sustained attention and task-difficulty from memory processes in a complex motor-learning paradigm. Well studied and novel finger movement sequences of different task-complexity (relatively simple vs. complex) had to be executed by healthy subjects. It was found that frontal midline theta increased with task-demand which is well in line with results about frontal EEG theta activity and sustained attention (Pennekamp et al., 1994; Gevins et al., 1997; Makeig et al., 2004a,b; Gomarus et al., 2006). This attention-related increase of theta activity could be localized into the anterior cingulate gyrus and the cingulate motor area. However, frontal midline theta did not dissociate between learned and novel motor sequences (see Fig. 3a). Long-range theta phase coherence on the other hand was stronger in the novel conditions compared to learned sequences independent of task-difficulty (Fig. 3b). During the execution of novel sequences a variety of sensory information had to be integrated into working memory which was not the case for the well studied sequences. This explains why fronto-parietal theta phase coherence was higher in the novel conditions. These results (Sauseng et al., 2007a) again highlight the very specific integrative function of theta long-range phase coherence/phase coupling in working memory processes. They further suggest that theta phase coherence can yield information about central executive functions that cannot be addressed by EEG amplitude estimates alone.

It was discussed by Sauseng et al. (2002, 2005a, 2006, 2007a) that fronto-parietal coupling during central executive functions of working memory is mainly established at theta frequency when the cognitive task requires some interfacing with other memory systems. If, however, the task does not have any integrative memory component but is a pure (visuo-spatial) working memory task one might more likely find effects in the upper alpha frequency band (around and beyond 10 Hz), as upper alpha EEG activity is sometimes linked to visuo-spatial information processing (Klimesch et al., 2003; Sauseng et al., 2005b,c; Thut et al., 2006; Rihs et al., 2007). Sauseng et al. (2005b) ran a visuo-spatial working memory task without any long-term memory component. Subjects either had to retain three spatial positions on a screen in memory for 2 s or in addition had to mirror the positions around the centre of the monitor (retention plus additional mental manipulation of the retained information). It was found that only during the condition with high demand of top-down processing (manipulation condition) prefrontal and parietal alpha amplitudes and also individual alpha peak frequency aligned resulting in a state of 'alpha equilibrium'. In this state of aligned alpha activity increased coupling between prefrontal and parietal electrode sites were found at upper alpha frequency. Using cross-correlations it was demonstrated that in the manipulation condition there were latency shifts from anterior to posterior, indicting information flow from the prefrontal to higher visual cortex. This was not the case in the pure retention condition. This shows that similar connectivity patterns as were found for theta frequency during central executive functions associated with integration of working and long-term memory processes were obtained at alpha frequency during top-down processing in a pure working memory task. This interpretation is underpinned by unpublished data from Sauseng and co-workers. They ran a comparable task as in Sauseng et al. (2005b) with the exception that verbal material (letters) was used instead of visuo-spatial stimuli. Healthy subjects either had to retain three consonants for 2 s or in addition to retention had to order the letters alphabetically. In the latter condition more top-down processing was required than during pure retention. Additionally, during alphabetical ordering long-term memory had to be accessed (which was not necessary in the manipulation condition of the visuo-spatial task reported in Sauseng et al., 2005b). The interesting finding was that in the manipulation condition using verbal material fronto-parietal long-range coupling was found at theta frequency (in accordance with the findings regarding integration of long-term and working memory functions reported above) whereas for the visuo-spatial task (Sauseng et al., 2005b) fronto-parietal connectivity was observed at upper alpha frequency.

However, alpha coupling between frontal and parietal brain regions was also reported to be relevant for visuo-spatial attention (Sauseng et al., 2005c). There, participants had to covertly shift their attention to a visual hemi-field which was cued by an arrow in each single trial. This was followed by presentation of one of two targets which had to be classified. Sauseng et al. (2005c) could show that already approximately 200 ms prior to target presentation, thus, in the time window in which visual attention was directed to the cued hemi-field, phase coherence in the upper alpha frequency band between a mid-frontal electrode site and parietal electrode sites overlaying the hemisphere contralateral to the attended visual field increased. In invalidly cued trials where visual attention had to be redirected after target presentation this was also indicated by a reconfiguration of the fronto-parietal phase coupling. Alpha amplitudes at posterior electrode sites contralateral to the attended visual hemi-field showed attention-related decrease indicating local activation. It was thus concluded that fronto-parietal phase coherence might be associated with the control of cortical activation level in higher visual areas establishing sustained biasing and attention-related amplification of neural responses to anticipated targets.

To sum up this section, we have argued that depending on whether there is interaction with long-term memory or not, interregional phase coupling between the prefrontal cortex and posterior brain areas either at theta or at alpha frequency play an important role for central executive functions in working memory. Thereby, phase coherence can help to disentangle cognitive processes which cannot be dissociated solely using EEG amplitude information. Also control functions during the direction of attention were reflected by phase coupling at alpha frequency between frontal and posterior brain areas.

2.2. Phase synchronization between oscillations of different frequency

When we assume that different cognitive systems, such as working memory, long-term memory, attention, perception and so on, are related to neuronal networks of different size and distribution then it should be clear that interaction of such systems need to be reflected by coupling between the underlying neural networks. As networks of different size are supposed to oscillate at different frequencies (larger networks generate slower frequency) such interaction as described above is to be found with cross-frequency phase synchronization in the human EEG. With a few exceptions (e.g., Schack et al., 2002; Schack and Weiss, 2005; Palva et al., 2005; Mormann et al., 2005; Demiralp et al., 2007a,b; Canolty et al., 2006; Sauseng et al., 2008) there are hardly any research reports demonstrating the relevance of phase synchronization across frequencies in the human brain for cognitive processes. The high temporal preciseness of synchronization between oscillations of different frequency can potentially explain how information between memory systems can be exchanged in the human cortex.

Basically, there are a few different kinds of phase interaction between frequencies which have been reported in animals and/or humans. One of them is that the instantaneous phase of a slower

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oscillation modulates the amplitude of a higher frequency. A nice example for this was described by Lakatos et al. (2005). They found that in the macaque brain there is a hierarchical interaction between slow and fast oscillations of the local field potential and multiunit activity. Already in a resting state instantaneous phase of delta activity modulated amplitude of theta frequency. At theta, on the other hand, there was also a bursting phase at which gamma amplitude and multiunit activity was increased. Multiunit activity, however, additionally was associated with the instantaneous phase of gamma activity. The authors argued that this hierarchical organization of oscillatory brain activity enabled the neural system to be precisely tuned for stimulus processing when only the slowest frequency reset its phase. A relation between theta phase and gamma amplitude was also consistently found in the human brain (Mormann et al., 2005; Demiralp et al., 2007a,b; Canolty et al., 2006). This holds true for memory processes in particular. But theta phase was also reported to interact with EEG alpha amplitudes in humans (Sauseng et al., 2002). When considering that upper alpha oscillations in humans are associated with long-term memory retrieval (for review see, e.g., Klimesch, 1997; Klimesch et al., 2007a) and theta is relevant for executive functions of working memory and interfacing between memory systems it is evident that theta and alpha oscillations should interact in combined working and long-term memory tasks. Sauseng et al. (2002) ran an experiment in which visual line drawings first were encoded into long-term memory. In a later part of the experiment (about 30 min after encoding) the studied items had to be retrieved from long-term memory and re-loaded into working memory for later semantic comparison of the retrieved pictures. Sauseng et al. (2002) found that travelling theta waves spread from anterior to posterior electrode sites during retrieval attempts. At the time point when the visual item was retrieved the direction of travelling theta was reversed, and theta was spreading from posterior to anterior sites. Interestingly, exactly at the time point at which theta travel direction reversed, upper alpha power started to decrease, indicating the successful attempt of memory retrieval. Moreover, the latency of theta reversal correlated with individual retrieval performance. Thus, this highly specific cross-frequency interaction between theta phase and alpha amplitude suggests being a neural correlate of complex integrative interplay between long-term and working memory in the human brain.

A somewhat different approach of phase interaction between oscillations of different frequencies is to look at the stability of phase differences across frequencies and trials. So-called cross-frequency phase synchronization or m:n phase synchronization is a relatively new method, but there are some recent publications on this phenomenon in the human brain (Schack et al., 2002, 2005; Palva et al., 2005; Sauseng et al., 2008; Sauseng et al., submitted-a,b). Using such direct estimate of phase interaction, namely cross-frequency or m:n phase synchronization, Schack et al. (2005) reported findings highly consistent with the ones by Sauseng et al. (2002). In a working memory paradigm Schack and co-workers found a strong memory-load dependent increase of phase coupling between prefrontal theta and posterior alpha activity. Prefrontal alpha to parietal theta phase synchronization on the other hand was decreased. These findings were interpreted as frontal theta reflecting executive processes of working memory and posterior alpha activity as correlate of reactivated long-term memory traces (Ruchkin et al., 2003). Following this interpretation, the interaction between (frontal) theta and (posterior) alpha phase might indicate the central executive of working memory accessing long-term memory contents, and thus this cross-frequency phase information seems to be associated with the interfacing between working and long-term memory (Schack et al., 2005). Sarnthein et al. (2005) also found phase synchronization between theta and higher frequencies during working memory processing. In patients suffering from neurogenic pain the authors recorded the local filed potential from the thalamus. Sarnthein and collaborators observed increased bi-coherence between theta and beta frequency when patients were counting backwards compared to a resting condition. This indicates that similar working memory-related effects on cross-frequency phase synchronization as found in the cortex can also be observed in the thalamus.

For working and short-term memory processes the relevance of phase synchronization or nesting of theta and gamma oscillations have been discussed (Lisman and Idiart, 1995; Jensen and Lisman, 1996, 1998, 2005). Recently, such a phenomenon has been reported in the human EEG. Schack et al. (2002) found phase synchronization between theta and gamma frequency at prefrontal cortices during a continuous word recognition experiment. Palva et al. (2005) reported synchronization between gamma and alpha (which is slightly faster than theta) during a sustained working memory task. Due to technical reasons, Palva and co-workers did not analyze theta to gamma coupling. It might be the case that effects would have been even stronger at this frequency pair. Sauseng et al. (2008, submitted) also highlight the relevance of theta–gamma phase synchronization for memory processes. Sauseng and collaborators (2008) showed that the matching of information held in working memory and incoming sensory information was associated with distributed theta activity in a fronto-parietal network. This network reflected memory-related top-down activation and its phase was locally synchronized with posterior parietal gamma oscillations. Moreover, this effect was amplified by directed visuo-spatial attention. In another recent study Sauseng et al. (submitted-a,b) demonstrated that memory-related theta–gamma phase synchronization in the parietal cortex was modulated by short-term memory load. During a retention interval cross-frequency phase synchronization increased with the number of visual items which have had been retained in memory up to the load at which memory capacity had been reached (around three to four items) and then decreased again. In advance, the increase of theta to gamma phase coupling was predictive for individual memory capacity.

Thus, to sum up this part, phase synchronization across frequencies is informative about the interaction of different cognitive systems, such as long-term and working memory or the matching between memory traces and external sensory percepts. In addition, it might explain limitations of short-term memory.

2.3. Phase-locking to stimulus presentation

As outlined above a key property of oscillatory phase in the human EEG is the high temporal preciseness at which it influences neural activity. Instantaneous phase of brain oscillations can be considered as control mechanism for the timing of neural firing (for review see, e.g., Klimesch et al., 2007a). Therefore, phase of oscillatory EEG activity and in particular its modulations are supposed to be of extreme importance for the processing of sensory stimuli in the brain.

A very common measure in the EEG is the ERP. Thereby stimuli are presented to the subject while the EEG is recorded and markers are set into the EEG trace whenever a stimulus is presented. Then a short epoch of EEG around each marker is used to average all these segments. This is based on the logic that in each trial there is a systematic brain response to a stimulus. However, this systematic response cannot be seen in the raw EEG, as there it is overlaid by a lot of unsystematic background activity (which is simply considered as noise). By averaging all the single epochs, only the systematic brain response should remain, but the background

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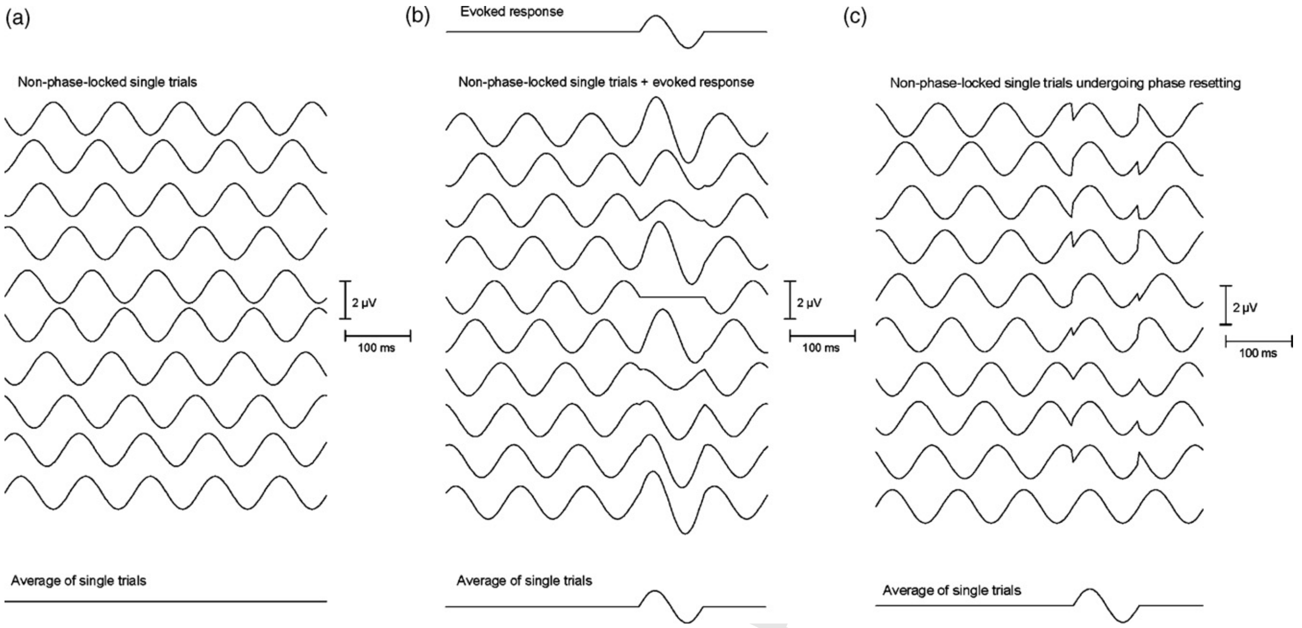

Fig. 4. General idea of evoked and phase rest model. (a) When a number of unrelated single trials which are not phase-locked to a stimulus are averaged a flat line will ideally be the result. (b) The evoked model assumes that in each single trial a constant evoked response is added onto the ongoing EEG. The background EEG is considered as noise completely unrelated to the event-related potential (ERP). When the single trials composed of the background EEG and an additive evoked response are averaged the event-related potential which exactly reflects the original evoked response will result. (c) The phase reset model suggests that the event-related potential is generated by a phase resetting of oscillatory background EEG. Without any additive evoked response an ERP will arise when single trials are averaged. Figure taken from Sauseng et al. (2007b).

EEG should approach zero (see Fig. 4). Classically this 'systematic brain response' is considered as an additive evoked response with a fixed latency and fixed polarity, completely independent of the ongoing (background) EEG, and that ERP components (the peaks in the remaining averaged ERP) are generated by such evoked responses. However, since already 30 years there has been the idea that the ERP might (at least in part) be generated by a phase reset of ongoing oscillatory EEG activity (e.g., Sayers et al., 1974; Brandt and Jansen, 1991; Brandt et al., 1991; Jansen and Brandt, 1991; for a comprehensive review see the pioneering work by Basar, 1999a,b; for the principle idea of the phase reset model see Fig. 4). In the last few years there has been a revival of the 'phase reset model' of ERP generation since a publication on this topic by Makeig and co-workers (Makeig et al., 2002; see also 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, 2006; Kruglikov and Schiff, 2003; Makeig et al., 2003; 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; Yamagishi et al., 2003). However, although there have been a great number of articles published arguing for or against phase resetting there is still no clear evidence for either the phase reset nor for the classical evoked model. Some of the used methods to investigate phase resetting were critically analyzed and evaluated (Yeung et al., 2004, 2006; Sauseng et al., 2007b). Yeung et al. (2004, 2006) and also Sauseng et al. (2007b) conclude that most of the methodological approaches which yield evidence for the phase reset model actually cannot dissociate between phase resetting and evoked model. This critique, however, also can be applied to research reports arguing for the classical view of ERP generation. For instance, Hanslmayr et al. (2007) did a simulation of data based on real EEG to demonstrate that the classical idea of ERP generation by a linear additive evoked response was not correct. The debate of ERPs either being generated by phase resetting of oscillatory brain activity or an additive evoked response is, however, still ongoing and is summarized in Sauseng et al. (2007b). There the authors document that by now there is no single research paper which can convincingly show that ERPs are generated by phase resetting of background EEG nor that they come from additive evoked responses. Nevertheless, the bulk of recent literature favoring the phase reset model suggests that the event-related potential is at least influenced in some way by oscillatory brain activity (Sauseng et al., 2007b). It is also argued in several recent papers that the generation of event-related potentials is based on both phase resetting and evoked response (e.g., Düzel et al., 2005; Fell et al., 2004; Fuentemilla et al., 2006; Mazaheri and Picton, 2005; Min et al., 2007). But information about the proportion of these two mechanisms is still lacking.

However, why is it important to know whether the ERP is generated by phase resetting or not? Which information could phase-locking to stimulus presentation provide for cognitive sciences? And what can we learn from phase resetting about the human brain? Sometimes one finds distinct cognitive processes that cannot be disentangled using physiological parameters such as the event-related potential. Roehm et al. (2004) demonstrated that phase-locking to stimulus onset can be helpful in dissociating neuronal correlates of such cognitive functions. In addition, a phase resetting approach can be used to integrate knowledge from the analysis of brain oscillations and from ERP research. For instance, Klimesch et al. (2004a) could show that subjects exhibiting more phase resetting of alpha activity in a memory task had better memory performance. This is in good agreement with findings regarding memory performance and ongoing EEG alpha activity. There was also a positive correlation between alpha activity and cognitive performance reported (see, e.g., Doppelmayr et al., 2002; Klimesch, 1999). In a recent article Klimesch et al. (2007b) found that stimulus-locked alpha phase and early ERP components had a very similar topographical distribution, spatio-temporal evolution and interindividual prop-

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erties. As early evoked EEG alpha activity has been related to basic categorization of visual input and inhibitory control of brain activity (Klimesch et al., 2007a) this interpretation can now be applied to effects of the P1 ERP component. And actually, similar functions as suggested by Klimesch et al. (2007a,b) for early alpha activity were found for the P1 in the visual event-related potential (Taylor, 2002).

Another example of how phase-locking to a stimulus can be informative about neural and cognitive processes is a recent work by Gruber et al. (2005). Using a phase-locking index (Schack and Klimesch, 2002) Gruber and co-worker first determined all frequencies up to 20 Hz that showed significant phase reset in response to a probe item during episodic memory retrieval. However, the phase-locking index alone gives no information about the mean direction of the instantaneous phase after phase resetting. Therefore, the authors also obtained the instantaneous phase angle for all time-frequency bins that showed significant phase-locking. The final stage was then to determine all remaining frequencies (with significant phase-locking) that showed similar mean direction of the instantaneous phase at the same time, e.g., 2, 4.5 and 13 Hz frequency bins all showing significant phase-locking and instantaneous phase angle of, for instance, about 90° at the same time frame post-stimulus. When several frequency bins showed this effect of similarity in (significant) mean direction of phase Gruber et al. called this instantaneous phase alignment (IPA). The results from the experiment suggested that the P1 ERP component (a positive component around 100 ms) was generated by phase alignment of broad alpha frequencies, whereas the N1 component (negative peak at about 170 ms) originated from alignment between theta and alpha frequencies (theoretically this was already suggested by Klimesch et al., 2004). Therefore, it can be assumed from the results by Gruber and collaborators that during the retrieval of information from episodic memory there is first a reactivation of a long-term memory trace (reflected by the effect at alpha frequency in the P1 time window) which is transferred to working memory in a later time window, reflected by the evoked coupling and phase alignment of alpha and theta frequencies. Thus, this approach yields knowledge about the interaction between memory systems and neural networks at a very high temporal preciseness, which is difficult to establish with other methods. Recently, the results from Gruber et al. (2005) have been replicated using intracranial recordings in epileptic patients (Mormann et al., 2005).

As extensively discussed in Sauseng et al. (2007b) phase-locking to external events can bear important information about cognitive processes, in particular their temporal coordination in the brain. And it can bridge the gaps between research about oscillatory brain activity and event-related potential studies. However, the validity of the phase reset model on which the whole approach is based can still be put into question.

3. Phase synchronization and behavior: merely correlative or causal?

Many of the above referred studies suggest that phenomena of phase synchronization are the underlying neural mechanisms of certain cognitive processes. Formally, it is not clear whether the association between these electrophysiological mechanisms and cognitive functions is of correlative or causal nature. However, there are some psychopharmacological and some clinical studies that provide evidence for the causal nature of phase synchronization as neural substrates of cognitive behavior. For instance, it was reported that in mild cognitive impairment and Alzheimer's disease there is reduced interregional phase coupling which is associated with degree of memory loss (e.g., Stam et al., 2003; Jeong, 2004; Babiloni et al., 2006). Memory impairment in the aging brain and Alzheimer's disease is associated with cholinergic hypofunction. Administration of cholinergic antagonists was found to lead to decreased interregional phase synchronization (Wink et al., 2006). Furthermore, muscarinic blockade was shown to reduce interaction between theta phase and gamma amplitude in the hippocampus of the mouse (Hentschke et al., 2007). All these studies suggest that phase synchronization plays a causal role in memory processes. Recently, Demiralp et al. (2007a,b) reported increased phase-locking to stimulus onset at gamma frequency in subjects with a polymorphism resulting in reduced dopamine transporter expression. This polymorphism leads to increased extracellular dopamine level which is associated with a prefrontal target detection mechanism in attentional functions. Interestingly, enhanced phase-locked gamma activity was only found in response to targets that had to be detected and not in distractor items. This suggests a causal role of phase-locking in attentional processing. However, to answer the question about causality of phase synchronization as neural substrate of cognitive functions more research on this topic is needed. More studies are required which selectively disrupt phase synchronization (using pharmacological or neurostimulation approaches) and evaluate its impact on cognitive behavior.

4. General conclusions: do brain oscillatory phase measures bear any new information about cognitive processes?

As outlined in the previous section, we find phenomena of phase synchronization in the human EEG (i) across brain sites, (ii) across frequencies and (iii) towards onset of external events. Each of these EEG responses yields important information that is not contained in any other measure of brain activity. As discussed above, the advantage of phase measures in the human EEG is its high temporal preciseness. Phase synchronization seems more tangible to measure neural communication on different spatial scales *per se* than do any other non-invasive brain activation estimates.

The connectivity between brain areas can be estimated by EEG phase coherence. There is no doubt anymore that activation of brain networks explains normal and abnormal brain processes and their behavioral outcome better than the reckoning of activity only in isolated brain regions (see also Schnitzler and Gross, 2005 for review). As the EEG signal can easily be separated in the frequency domain and also the temporal preciseness of electrophysiological measures is extremely good it is highly suitable for connectivity studies. Due to their poor temporal resolution and little information about the physiological origin of the BOLD signal, correlation approaches in functional magnet resonance imaging are far less feasible for the investigation of connectivity in the brain than is phase coherence in the EEG. In Section 2.1 it has already been lined out that interregional phase coupling can be used to disentangle neural substrates of cognitive processes that cannot be dissociated with other methods alone. For instance, it was shown that long-term memory retrieval can be separated from sustained attention, or central executive functions of working memory can be traced using phase coherence in the EEG. In addition, interareal phase coupling can be informative about the (top-down) control of the level of cortical activation in working memory and attention processes. Cross-frequency phase synchronization on the other hand is a highly potent measure for investigating the interaction between cognitive systems. In Section 2.2 it was shown that phase synchronization between theta and alpha oscillations reflects the exchange of information between long-term memory and working memory. Theta to gamma phase coupling on the other hand can be found during matching of stored with incoming information. Such interaction between different neural systems can hardly be shown with any other neuroscientific approach. And at last, it was demonstrated above (Section 2.3) that phase-locking to stimulus presentation yields important information about the temporal order of cognitive processes.

Taken together, the studies presented in this review should show that phase synchronization in the human EEG bears important information for the understanding of cognitive and neuronal processes. Phase coupling, either across brain regions, frequencies or to external stimuli reflect highly specific functions. Often these are much more meaningful and more instructive than other parameters, such as amplitude estimates in the EEG. It has been suggested above that most specific brain processes are controlled by the phase of oscillatory activity and its interplay with other oscillations. EEG amplitude, on the other hand, simply seems to reflect the level of general (rather unspecific) brain activation. It is assumable that phase synchronization approaches will play a very important role in future EEG research and in cognitive neurosciences as a whole.

Uncited references

Talk et al. (1999) and Yeung et al. (in press).

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