

Neuronal oscillations in gamma- and alpha-frequency bands: from object representations to sensory awareness

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Cover

A figurative synthesis of the framework advanced in this Thesis. Here, alpha-band-synchronized networks define a global workspace and gamma-band oscillations underlie sensory object representations. Alpha-gamma cross-frequency phase synchrony binds these “contents” of cognition into the focus of attention. Modified from the cover of *The Journal of Neuroscience*, April 13, Vol. 25(15), 2005. See also figure 1 (A2) of this thesis.

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Abbreviations

| | |
|-------------|--|
| A17 | primary visual cortex |
| A7 | visual association area |
| CF | Cross-frequency |
| cSI | Contralateral primary somatosensory cortex |
| cSII | Contralateral secondary somatosensory cortex |
| EEG | Electroencephalography |
| ERD | Event-related desynchronization |
| ERP | Event-related potential |
| ERS | Even- related synchronization |
| MEG | Magnetoencephalography |
| PLF | Phase-locking factor |
| SM | Sensorimotor region |
| TFR | Time-frequency representation |
| WM | Working memory |

1. Abstract

The synchronization of neuronal activity, especially in the beta- (14-30 Hz) /gamma- (30–80 Hz) frequency bands, is thought to provide a means for the integration of anatomically distributed processing and for the formation of transient neuronal assemblies. Thus non-stimulus locked (*i.e.* induced) gamma-band oscillations are believed to underlie feature binding and the formation of neuronal object representations. On the other hand, the functional roles of neuronal oscillations in slower theta- (4–8 Hz) and alpha- (8–14 Hz) frequency bands remain controversial. In addition, early stimulus-locked activity has been largely ignored, as it is believed to reflect “merely” the physical properties of sensory stimuli. With human neuromagnetic recordings, both the functional roles of gamma- and alpha-band oscillations and the significance of early stimulus-locked activity in neuronal processing were examined in this thesis. Study **I** of this thesis shows that even the stimulus-locked (evoked) gamma oscillations were sensitive to high-level stimulus features for speech and non-speech sounds, suggesting that they may underlie the formation of early neuronal object representations for stimuli with a behavioural relevance. Study **II** shows that neuronal processing for consciously perceived and unperceived stimuli differed as early as 30 ms after stimulus onset. This study also showed that the alpha band oscillations selectively correlated with conscious perception. Study **III**, in turn, shows that prestimulus alpha-band oscillations influence the subsequent detection and processing of sensory stimuli. Further, in Study **IV**, we asked whether phase synchronization between distinct frequency bands is present in cortical circuits. This study revealed prominent task-sensitive phase synchrony between alpha and beta/gamma oscillations. Finally, the implications of Studies **II**, **III**, and **IV** to the broader scientific context are analysed in the last study of this thesis (**V**). I suggest, in this thesis that neuronal processing may be extremely fast and that the evoked response is important for cognitive processes. I also propose that alpha oscillations define the global neuronal workspace of perception, action, and consciousness and, further, that cross-frequency synchronization is required for the integration of neuronal object representations into global neuronal workspace.

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3. Introduction

3.1 Neuronal synchrony and gamma-frequency band oscillations

Singer, Gray, and colleagues (Singer and Gray, 1989; Gray et al., 1989) observed that when neurons in the cat primary visual cortex with distinct receptive fields are jointly stimulated with one “perceptual” object, the action potentials of these neurons become synchronized. When, on the other hand, these neurons were stimulated by two separate perceptual objects, the firing rates remained unaffected but the synchrony was abolished. Since then, the strength of neural synchrony has been found to depend on the classical perceptual “Gestalt” grouping criteria such as vicinity, continuity, colinearity, and common fate (Kaniza, 1976) in cat and monkey cortices (Gray et al., 1989; Engel et al., 1991; Kreiter & Singer, 1996; Livingstone, 1996). The strengthening of neural

synchrony was found even when no, or only little, changes were observed in the simultaneous firing rates of the neurons (Castelo-Branco et al., 2000; Engel et al., 1991; Freiwald et al., 1995; Gray & Viana Di Prisco, 1997; Kreiter & Singer, 1995). These findings led to the “temporal correlation hypothesis” which posits that neural synchrony is essential in the binding of anatomically distributed processing and thereby in the formation of transient neuronal assemblies coding for perceptually coherent objects (Gray, 1999; Singer & Gray, 1995; Singer, 1999). As neural synchrony is often found with the neuronal network oscillations in the gamma-frequency band (30–80 Hz) (Castelo-Branco et al., 2000; Engel et al., 1991; Freiwald et al., 1995; Friedman-Hill et al., 2000; Gray & Viana Di Prisco, 1997; Herculano-Houzel et al., 1999; Kreiter & Singer, 1995; Fries et al., 2002; Maldonado et al., 2000; Siegel et

al., 2007; Womelsdorf et al., 2006), it has been proposed that especially the gamma oscillations underlie feature binding, perceptual grouping, and reflect in general, the periods of active information processing in the brain (Herculano-Houzel et al., 1999; Llinas & Ribary, 1992; Tallon-Baudry & Bertrand 1999).

3.2 Human gamma-band oscillations and the formation of object representations

In human electroencephalography (EEG) and magnetoencephalography (MEG) recordings, evoked (phase locked to stimulus onset) and induced (non-phase locked) gamma oscillations, occurring at 40–100 and 200–300 ms from stimulus onset, respectively, may be observed. It was demonstrated that both the amplitude (Eulitz et al., 2000; Lutzenberger et al., 1994; Herrman et al., 1999, Tallon-Baudry et al., 1996; 1997) and degree of the

large-scale synchrony (Rodriguez et al., 1999) of the *induced* gamma oscillations are correlated with ‘Gestalt’ or other cognitive stimulus properties such as coherence and meaningfulness. In the auditory modality, the semantic characteristics of speech are also reflected in the induced gamma oscillations (Pulvermüller et al., 1996). On the other hand, most investigations have reported that the *evoked* gamma oscillations are insensitive to such high-level stimulus properties in both the visual and auditory modalities (Bertrand and Pantev, 1994; Haenschel et al., 2000; Pantev et al., 1991; Pantev and Elbert, 1994; Tiitinen et al., 1994). Tallon-Baudry and Bertrand (1999) suggested that the induced gamma oscillations underlie the formation of neuronal object representations and mediate both the bottom-up and top-down facets of stimulus processing. At that time, there was

little evidence for a similar role for the evoked gamma oscillations.

A few later studies, however, showed that also the visual (Herrman et al., 1999; Spencer et al., 2003) and auditory (Knief et al., 2000; Palva et al., 2002/Study I) evoked gamma-band oscillations are sensitive to high-level stimulus features. Moreover, similarly to the induced (Tallon-Baudry et al., 1997) oscillations, attention enhances also the amplitudes of evoked oscillations (Fries et al., 2001b; Tiitinen et al., 1993). In addition, perceived and unperceived somatosensory stimuli, despite the fact that in that study these stimuli were physically identical, have been shown to evoke distinct gamma band responses (Palva et al., 2005a/Study II). Thus, there are noteworthy similarities between evoked and induced gamma-band oscillations, but, nevertheless, the role of evoked gamma response in the formation of

object representations has remained debated.

3.3 Gamma-band oscillations and higher cognitive functions

In line with the idea that gamma oscillations underlie feature binding and the formation of object representations (Tallon-Baudry & Bertrand 1999), gamma-band oscillations are present during working memory (WM) maintenance period both in humans (Howard et al., 2003; Osipova et al., 2006; Tallon-Baudry et al., 1998; 1999; 2001) and in monkeys (Tallon-Baudry et al., 2004). Gamma-band synchrony characterizes also conscious perception in human (Rodriguez et al., 1999; Meador et al., 2002; Schurger et al., 2006) and cat (Fries et al., 1997) recordings. In addition, gamma-band oscillations are modulated by attention both in humans (Bauer et al., 2006; Fries et al., 2001b; Gruber et al., 1999; 2002; Lutz et al., 2002; Muller et

al., 2000; Tiitinen et al., 1993; Tallon-Baudry et al., 2005; Vidal et al., 2005) and animals (Fries et al., 2001b; Steinmetz et al., 2000; Taylor et al., 2005). Thus gamma-band oscillations are present during, and likely to be involved in cognitive functions from feature binding to consciousness. However, oscillations in the alpha- (8–14 Hz) and theta- (4–8 Hz) frequency bands have not been associated with feature binding nor with the formation of object representations. In this thesis, the functional roles of alpha-frequency band oscillations, in particular, are further examined and discussed.

3.4 Alpha amplitude dynamics

Hans Berger (1929; 1930) was among the first to find EEG-rhythms in the alpha- and beta- (14–30 Hz) frequency bands and noticed that the parieto-occipital alpha rhythm is attenuated by eye opening and mental effort. Adrian & Matthews (1934) suggested that

alpha oscillations have an idling function and reflect an “alert but still” brain state. In addition, it was noticed that also visual stimuli (Pollen and Trachtenberg 1972a), movements (Gastaut, 1954; Chatrian, 1959) and increased attentiveness (Pollen and Trachtenberg, 1972b) attenuate the alpha activity. Ray & Cole, (1985a, b) proposed that the function of alpha-band oscillations is, in fact, the inhibition of sensory information processing. Later, Pfurtscheller et al. (1992) suggested that the alpha-amplitude suppression after sensory stimulation and during movement execution indicates the time period of active information processing, whereas simultaneous alpha enhancement in the surrounding cortical areas reflects an idling state that is unrelated to the sensory processing or movement execution. More recently Klimesch, Pfurtscheller, and co-workers (Neuper & Pfurtscheller, 2001;

Klimesch, 1996; Pfurtscheller et al., 1996; 2003; Pfurtscheller & Lopes da Silva, 1999) have argued that the function of alpha-band oscillations is to inhibit and disengage task-irrelevant cortical areas. Along these lines Klimesch et al., (2007) suggested that alpha oscillations reflect inhibitory top-down control process.

A large number of recent studies corroborate the original observations of decreased alpha oscillations after sensory stimulations. The performance and imagery of movements (Pfurtscheller, 2000) and the electrical stimulation of a medial nerve (Nikouline et al., 2000; Stancak et al., 2003) lead to conventional alpha amplitude suppression over the somatomotor regions. In the visual modality, visual stimuli suppress alpha oscillatory activity in the occipital cortex contralateral to the attended visual hemifield (Thut et al., 2006; Worden et al., 2000) and in the

parieto-occipital region (Vanni et al., 1997; Hari et al., 1997). The stimulus-induced suppression of the alpha-band amplitude usually begins at around 200-400 ms after stimulus onset and its duration strongly depends on the stimulus parameters and the subject's performance and effort (Hari and Salmelin, 1997).

Intriguingly, strengthened alpha-band amplitudes can be detected during internal tasks such as mental imagery (Salenius et al., 1995; Hari & Salmelin 1997; Cooper et al., 2004; 2006) and mental calculation (Palva et al., 2005b/Study IV). In addition, WM tasks are also associated with enhanced alpha-band amplitudes during the memory retention period (Bauer et al., 2006; Busch and Herrman 2003; Jensen et al., 2002; Onton et al., 2005; Sauseng et al., 2005; Schack and Klimesch 2002). Intriguingly, in these tasks, the amplitude of parietal alpha-band oscillation is often correlated with

the working-memory load, being greater when a larger number of objects are memorized (Busch and Herrman, 2003; Jensen et al., 2002; Onton et al., 2005) or when the WM task is more demanding (Sauseng et al., 2005). Klimesch et al. (2007) suggested the large amplitude alpha oscillations during retention period inhibit the memory retrieval of memorized items and that the retrieval would later be reflected in the amplitude suppression that follows the second stimulus presentation. I argue here that the alpha-band oscillations during the retention period, however, belong to the network activity that sustains the neuronal representations of memorized items.

In line with this idea Sauseng et al. (2005) showed that alpha amplitudes are enhanced in the prefrontal while decreased in the occipital cortex and suggested that these results argue against the inhibition hypothesis. On the other hand, in the other WM studies

Bauer et al., (2006), Busch and Herrman (2003), and Schack and Klimesch (2002) interpreted the enhanced alpha amplitudes to be in line with the inhibition hypothesis. Interestingly, a recent spatial WM study (Medendorp et al., 2007) demonstrated decreased alpha amplitudes contralateral to the memorized hemifield. These results are very similar with those showing alpha amplitude suppression contralateral to the attended visual hemifield (Thut et al., 2006; Worden et al., 2000) and were interpreted as suggesting that alpha-amplitude suppression is related to the dorsal visual stream processing (Medendorp et al., 2007).

Taken together, the studies on alpha amplitude appear to provide contradictory results on the functional role of the alpha-band activity. This might, in part, be caused by the difficulties in inferring physiological or functional conclusions on the basis of

amplitude changes. In addition, many of the conclusions pertaining to the inhibition hypothesis have been based on EEG recordings, in which, it is not straightforward to identify task-relevant or -irrelevant cortical regions because of spatial smearing of the scalp potential.

It is often assumed that the overall activity level is approximately constant and that the amplitude changes are caused by changes in neuronal synchrony. The amplitude decrease is hence called “event-related desynchronization” (ERD) and the amplitude increase “event-related synchronization” (ERS) (Pfurtscheller, 2003). However, in the absence of changes in actual synchrony, the field amplitude may change if the number of neurons entrained to the oscillation is changed or if phase relationships of sub-populations change. Moreover, considerable phase ordering may take place in the absence of amplitude changes (Palva et al., 2005/Study II) or even

during simultaneous amplitude suppression (Mima et al., 2001; Halgren et al., 2002). Thus the neuronal-level significance of macroscopic amplitude measurements depends on the measurement method and the associated facts and assumptions on the signal generation mechanisms.

On the other hand, the presence of field-signal phase synchrony indicates the presence of neuronal-level spike synchrony, regardless of the recording method and level of inspection. This is relevant, as the spike timing has been suggested to be critical in neuronal communication (Traub et al., 1998; Fries, 2005). Interestingly, accumulating evidence on the alpha phase dynamics suggests that alpha oscillations are related to attention (Halgren et al., 2002; Henslmayr et al., 2005; Kolev et al., 1999; Mima et al., 2001; vonStein et al., 2000) and consciousness (Gail et al., 2004; Palva et al., 2005a/Study II)

rather than to inhibition or disengagement of sensory information processing (Neuper & Pfurtscheller, 2001; Klimesch, 1996; Pfurtscheller et al., 1996; 2003; Pfurtscheller & Lopes da Silva, 1999). The issue of alpha oscillations' functional role in the light of available amplitude and phase data is discussed in Study V of this thesis.

3.5 Early stimulus processing

It is often thought that stimulus-evoked activity “merely” reflects the low-level stimulus processing of physical stimulus dimensions and should thus be ignored in studies examining higher cognitive functions. However, high-level neural representations of behaviourally relevant stimuli such as phonemes (Näätänen et al., 1997), complex visual scenes (Thorpe et. al., 1996), faces (Linkenkaer-Hansen et. al., 1998), and visually presented words (Asadollahi & Pulvermuller, 2001,

Pulvermuller et al., 2001), are available already 100–150 ms after stimulus onset, indicating that the stimulus-related processing for the behaviourally relevant and simple stimuli should be performed as early as during the time-period of the evoked response.

The studies of oscillatory activity in humans both underscoring the representational role of the induced gamma oscillations (Tallon-Baudry & Bertrand 1999) as well as the relevance of the amplitude suppression after sensory stimulation (Pfurtscheller, 1996; Pfurtscheller & Lopes da Silva, 1999) are based on findings that are prominent from ~200–300 ms onwards after stimulus onset, *i.e.*, clearly after the evoked response. This is quite late if one considers the fact, that for the behaviourally relevant or simple stimuli, the formation of object representations should be completed as early as during the first 100–150 ms from

stimulus onset. Therefore, the evoked gamma oscillation might well be suitable for participating in the formation of the neural representations for such stimuli. In addition, one might question whether, the late alpha amplitude suppression has relevance to stimulus processing *per se*.

3.6 Does cortical information processing require cross-spectral integration?

Taken together, neuronal oscillations in the gamma and alpha bands have been suggested to play completely distinct or even complementary roles in stimulus processing. It has been thought, that the oscillations in the gamma band characterize periods of active information processing and underlie feature binding (Singer, 1999) and the formation of object representations (Tallon-Baudry & Bertrand, 1999), whereas the presence of large-amplitude alpha oscillations indicates the inhibition

or disengagement of inactive cortical areas (Klimesch, 1996; Pfurtscheller, 2003).

However, as suggested by studies on alpha phase dynamics, alpha oscillations might be critical in the mechanism of attention (Babiloni et al., 2006; Halgren et al., 2002; Henslmayr et al., 2005; Kolev et al., 1999; Mima et al., 2001; vonStein et al., 2000) and consciousness (Gail et al., 2004, Palva et al., 2005a/Study II). Accordingly, simultaneous alpha and gamma oscillations may be observed during stimulus perception (Palva et al., 2005a/Study II; Siegel & König, 2000; Tanji et. al., 2003), attention (von Stein et al., 2000) and WM (Halgren et al., 2002). If the alpha and gamma oscillations were to cooperate in active neuronal processing, then there would evidently be a problem of how the integration of these *spectrally* distributed processes was achieved. The need for the integration over

multiple frequency bands during unified cognitive operations has been recognized also earlier (Engel & Singer, 2001; Idiart & Lisman, 1995; Varela et al., 2001), and has been approached by multiple modelling studies (Jensen & Lisman, 1996; 1998; 2005).

The mechanism for cross-spectral integration could be mediated by amplitude co-variance, or by cross-frequency phase interactions. The presence of nested oscillations in cortical processing has been shown by various studies (Eckhorn et al., 2004; Schack et al., 2002, Schanze, & Eckhorn, 1997; Vanhatalo et al., 2004, von Stein et al., 2000). However, one may also have cross-frequency (CF) phase interactions in the form of $n:m$ -phase synchrony, where the integers m and n define the ratio of the two frequencies (Tass et al., 1998; 2003). Such $n:m$ cross frequency phase synchrony was not observed between cortical oscillations (cf. Tass et al., 1998; 2003) by the

time of Study IV however, and therefore this cross-spectral binding mechanism was further examined and found to exist between cortical oscillations (Palva et al., 2005b).

4. The aims of the thesis

This thesis consists of 5 studies in which the functional roles of both the gamma and alpha oscillations as well as their mutual $n:m$ phase synchrony were investigated.

The aim of the first study (Study I) was to determine whether the evoked gamma oscillations could be sensitive to high-level stimulus features and could thus underlie the formation of early neural representations.

Study II aimed to determine the neural correlates of sensory awareness in terms of event-related phase and amplitude dynamics.

Further the aim of the Study III was to determine whether prestimulus oscillations could affect the perception of sensory stimuli.

Study IV, in turn, aimed at determining (i) whether phase synchrony between oscillations in distinct frequency bands may be observed, and if so, (ii) whether this CF synchrony is sensitive to cognitive tasks demands and could thus provide a means for cross-spectral integration.

The final goal of the present thesis work was to compile an integrated view on the observations made, especially on those pertaining to the alpha oscillations (Studies II, III and, IV). Their relevance is analysed and discussed in the fifth study (Study V) of this thesis.

5. Methods

5.1 Subjects and measurements

In all studies, subjects were healthy volunteers aged between 18-32 years and with a background of no neurological diseases. Cortical activity was recorded using either a 102- or a 306-channel whole-scalp

magnetoencephalography (MEG) instrument (Neuromag Elekta, Helsinki) in an electrically and magnetically shielded room. The signals from the planar gradiometers were used for data analyses. Electro-oculograms (EOGs) were recorded for artefact rejection and the responses (Studies II, III) were recorded with thumb-movement electromyograms.

5.2 Stimuli & Paradigm

Stimuli in Study I were physically comparable speech and non-speech sounds that were binaurally presented through headphones at 60 dB above the individual hearing level. Subjects watched a silent video during the recordings. Further, in studies II and III, stimuli used were weak constant-current electrical pulses delivered to the left, right, or both index fingers equiprobably in a semi-random order with intensities adjusted to the threshold of detection, so that only 30-40 % of

the stimuli were perceived. The stimulus-onset-asynchrony varied randomly between 3 to 4 seconds. During the recordings, the subjects sat eyes closed and reported all perceived stimuli with a thumb switch. Finally, in a Study IV, the subjects were instructed to sit eyes closed and to perform continuous mental arithmetic task either with two or three numbers in order to modify the number of items in the focus of attention/ WM, or to think of nothing (rest/meditate). In the mental arithmetic tasks, the load of attention/ WM was near or at its capacity limits of $\sim 3 \pm 1$ (see Luck & Vogel, 1997; Cowan 2000), whereas the rest condition minimized the number of simultaneously maintained active neural representations in the focus of attention/ WM.

5.3 Data analyses

Evoked responses were obtained by averaging peri-stimulus epochs in time domain. They contain signal

components that are strictly time locked to the stimulus but include both the phase and amplitude information. *The phase locking* of the ongoing activity to a stimulus was quantified by first obtaining the continuous phase by wavelet or Hilbert-transform approaches and then estimating the phase-locking factor (PLF). *Non-stimulus-locked* components, “induced oscillations”, were characterized by averaging the signal amplitudes instead of the signals themselves. Continuous amplitude was obtained with Morlet wavelets or with conventional filtering and the Hilbert transform. *The quantification of CF-phase synchrony* was based on the estimation of the phase difference between the oscillations in distinct frequency bands followed by a statistical quantification of the uniformity of the phase difference distribution (Tass et al., 1998). An interested reader will find further methodological details in the original publications.

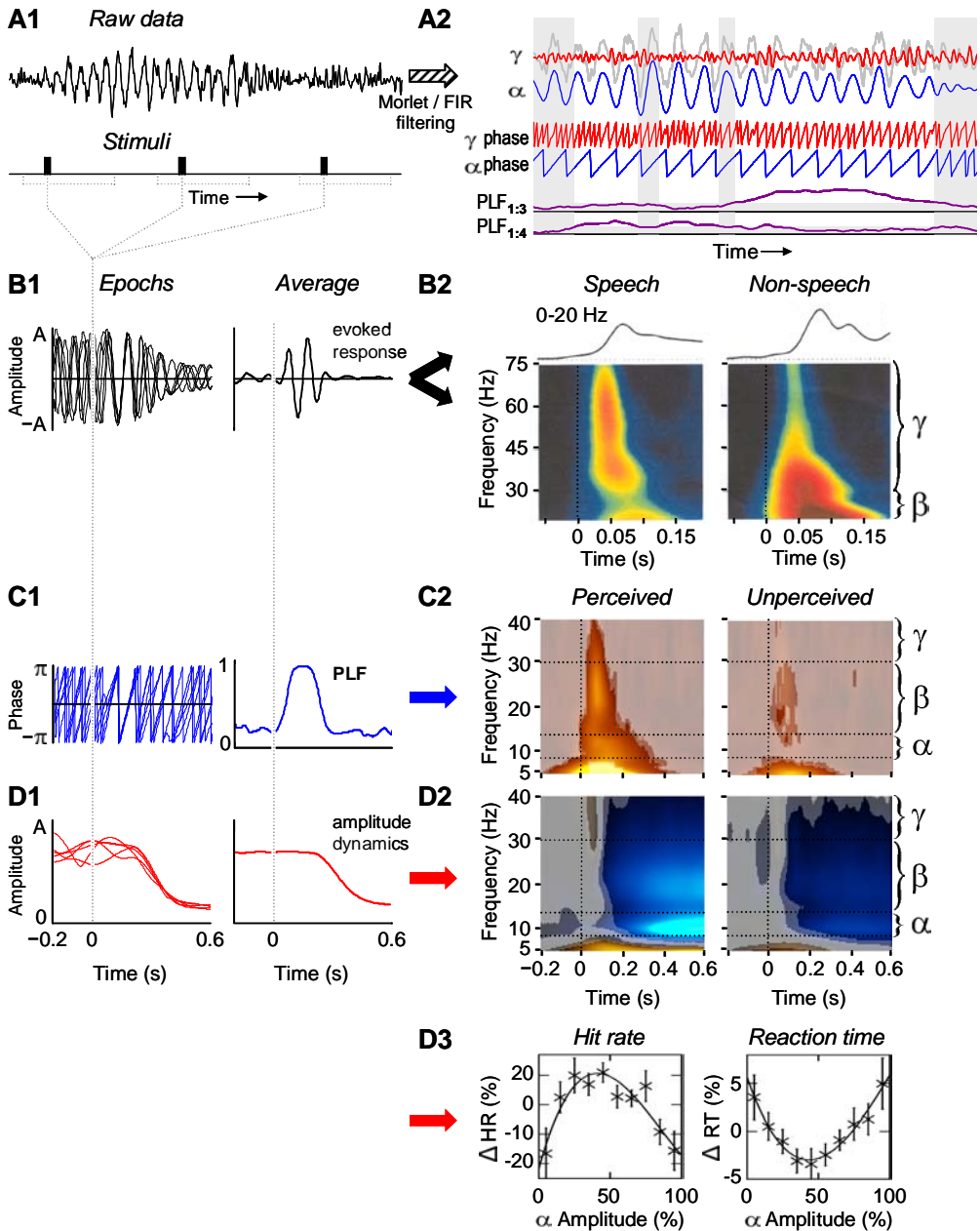
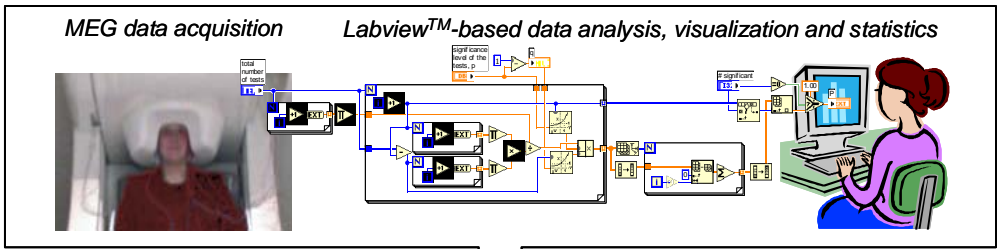


Figure 1. Overview of the methods and results of the thesis. All data were recorded with NeuroMag 122-channel (Study I) and 306-channel (Studies II-IV) MEG devices in a magnetically shielded room. After data acquisition, data were analyzed with custom Labview-based software on personal computers and workstations.

A1 Sample broadband (1-70 Hz) raw data from an MEG gradiometer over right occipital cortex. **A2** Raw data were filtered with FIR band-pass filters to isolate oscillations in distinct frequency bands (blue trace, α -band: 8-16 Hz, center frequency 10 Hz; red trace, γ -band: 24-50 Hz, center frequency 30 Hz; gray trace, broad-band: 1-70 Hz). Hilbert-transform was used to obtain the continuous phase of these oscillations (see α phase, γ phase). Hilbert-transform of the filtered data (= real part, X) gives its imaginary part, Y , which can be used to obtain the continuous phase, θ , and amplitude, A , with the equation $X + iY = Ae^{i\theta}$, where i indicates the imaginary unit. This complex representation of the data in time-frequency domain may also be directly achieved by convoluting the data with (complex) Morlet wavelets. CF-phase synchrony may take place among oscillations of which the frequency ratio is given by integers n and m so that $nf_x = mf_y$. CF-phase synchrony among alpha and gamma oscillations here was quantified for $n:m$ ratios of 1:3 and 1:4 using the PLF (see purple traces, PLF_{1:3} and PLF_{1:4}) within a 500 ms sliding window. PLF is given by $PLF = N^{-1}|\sum e^{i\theta_{xy}}|$, where N is the number of samples and the phase difference θ_{xy} is given by $\theta_{xy} = n\theta_x - m\theta_y$. PLF ranges from 0 (flat phase distribution - no synchrony) to 1 (perfect synchrony). The periods where statistically significant ($p < 0.05$) phase synchrony was *not* observed are identified with gray shading. The data show significant CF-phase synchrony between gamma and alpha band oscillations (Study IV). This type of phase synchrony was prominent between alpha and beta as well as between alpha and gamma oscillations. Importantly, phase synchrony among alpha, beta, and gamma oscillations was modulated by mental arithmetic tasks.

In addition to continuous tasks (Study IV), also auditory (Study I) and somatosensory (Studies II and III) stimuli were used in this thesis. Stimulus triggers in relation to raw data are schematically shown in A1. **B1** To investigate stimulus processing using event-related measures, peri-stimulus epochs of data are cut and averaged. An average of the epochs in time domain (= real part of the signal, see A2) gives the classical evoked response. **B2** The subjects were presented speech (/pa/) and physically comparable non-speech sounds during a video-watching task. The amplitudes of averaged responses (color coded: black, small - red, large) evoked by speech and non-speech sounds were estimated as a function of time and frequency with an array of Morlet wavelets and averaged across subjects and across the 10 gradiometers displaying largest beta/gamma band amplitude over the left auditory cortex in each subject. These data reveal that evoked beta- and gamma-frequency band (here 20-75 Hz) oscillations are distinct for speech and non-speech sounds whereas such a difference was not observed in the amplitude of evoked responses in the 1-20 Hz band. Thus, the evoked gamma-band oscillation is sensitive to high-level stimulus features (Study I).

C1 Phase locking of ongoing activity to stimulus onset can be quantified by using the PLF, as in A2, but “averaging” the phase values across the epochs instead of within a time window. **C2** The tips of subjects’ index fingers were stimulated with very weak electric constant-current pulses. Stimulus intensity was adjusted so that slightly less than half of the stimuli were perceived. The subjects’ task was to indicate the perceived stimuli with a prompt thumb twitch. The continuous phase of single epochs was obtained with an array of Morlet wavelets covering the frequency range of interest. From these data, the PLFs were computed separately for perceived and unperceived stimuli and for each of the 204 gradiometers. C2 shows the phase locking of ongoing activity in contralateral primary somatosensory cortex (cSI) to perceived and unperceived stimuli as a function of time and frequency averaged across the subjects. This data show that alpha- and gamma-band phase locking is correlated with

conscious perception (Study II). In frontal and parietal regions, phase locking of ongoing oscillatory activity was mainly found only for the perceived stimuli in the alpha-frequency band suggesting that the large-scale alpha-band-phase locking may subserve conscious perception.

D1 Continuous amplitude (see A2) obtained with the Hilbert transform or with Morlet wavelets is averaged over peri-stimulus epochs to yield an estimate of mean amplitude dynamics. **D2** Amplitude dynamics of cSI (as in C2). The amplitudes of alpha, beta, and gamma-frequency bands were suppressed by both perceived and unperceived somatosensory stimuli, the amplitude suppression being larger for the perceived stimuli (Study II). **D3** Single-trial correlation of somatosensory pre-stimulus alpha-band amplitude with behavioral performance. Hit rate (HR) is highest and the reaction time (RT) is fastest for stimuli preceded by intermediate amplitude values (Study III, note that Studies II and III are based on the same recordings).

5. Results

6.1 Distinct gamma-band evoked responses to speech and non-speech sounds in humans.

In Study I, we asked whether the evoked gamma-band component would reflect high-level stimulus features. We presented subjects with semi-synthetic speech and physically comparable complex non-speech sounds and recorded auditory evoked responses with MEG. We computed time-frequency representations (TFRs) of the amplitude of the evoked responses to both sounds (Fig. 1, B2) and found that the gamma oscillations to speech sounds peaked earlier over the left than over the right hemisphere, whereas

the opposite was true for the non-speech sounds. Moreover, the speech and non-speech sounds displayed distinct spectral characteristics: The gamma band amplitude was differentially lateralized for speech and non-speech sounds. The amplitude of the low-gamma (25–45 Hz) component was equal over the left and right hemispheres for the speech sounds, whereas it was larger over the right than left hemisphere for the non-speech sounds. Interestingly, however, the responses to speech sound also consisted of a higher gamma-band component at around 60 Hz of which the amplitude was considerably larger over the right than over the left hemisphere. Thus

several characteristics of the evoked gamma-band response were distinct for the speech and non-speech sounds and showed that even the evoked gamma oscillation, occurring as early as 40-100 ms after stimulus onset, is sensitive to high-level stimulus features.

6.2 Early neural correlates of conscious somatosensory detection.

In Study II, we examined the neural correlates of conscious somatosensory detection. We found that the broad-band (1–80 Hz) phase locking to the perceived and unperceived somatosensory stimuli differed as early as 30 ms after stimulus onset. Over the contralateral primary (Fig. 1 C2) and secondary somatosensory cortices (cSI and cSII, respectively) as well as over sensorimotor (SM) regions, the responses to the consciously perceived stimuli comprised of phase locking in the alpha as well as in the theta (4-7Hz), beta- (15-26 Hz), and gamma

bands. On the other hand, the responses to undetected stimuli were associated with phase locking in the theta and beta bands but did not show significant alpha-band phase locking. In addition, the alpha-band phase locking for the consciously perceived stimuli spread from the SM to frontal and parietal regions but the phase locking to undetected stimuli remained localized over the cSI. We found that also the phase locking in the gamma band was selectively present only for the consciously perceived stimuli. The gamma-band phase locking was, however, only very brief in duration and occurred only over cSI. Thus, our study showed that the conscious and unconscious processing of weak sensory stimuli diverged as early as at 30 ms after stimulus onset. In addition the study showed that large-scale alpha- phase locking was selectively correlated with conscious perception.

In order to relate these results to those of the other studies on alpha oscillations, we also analyzed the alpha-amplitude-dynamics for the consciously perceived and unperceived stimuli (Fig. 1 D2) and found that both the perceived and unperceived stimuli were followed by the well-known alpha amplitude suppression (Klimesch, 1996; Pfurtscheller, 2003) over the cSI, cSII, SM. This suppression was larger for the detected than undetected stimuli and began at termination of the phase-locked activity.

6.3 Prestimulus oscillations enhance psychophysical performance in humans

In Study III we examined whether oscillatory activity in the prestimulus period could affect the subsequent detection of weak sensory stimuli. We found that the presence of intermediate amplitudes of the alpha, beta, and gamma oscillations in the prestimulus period over the somatomotor

regions lead to highest detection rates (Fig1. D3). In addition, these intermediate amplitude values lead to the shortest reaction times (RTs) for the detected stimuli. However, over the parietal regions, the highest amplitudes of the alpha- and beta-band oscillations in the prestimulus period lead to the highest detection rates. This study thus showed that the stimulus detection is biased by prestimulus oscillatory activity and that oscillations in different anatomical regions may have qualitatively distinct impact on stimulus processing.

6.4 Phase synchrony among neuronal oscillations in the human cortex.

In Study IV we investigated whether $n:m$ -phase synchrony between the distinct frequency bands is present in the human cortex and, further, whether this synchrony would be modulated by cognitive task demands. The general goal was to address whether

n:m-synchrony between frequency bands could underlie cross-spectral integration.

We found that phase synchrony among beta/gamma- and alpha-band oscillations was a salient characteristic of ongoing activity in the human cortex (Fig. 1 A2). Furthermore, the synchrony between the alpha and beta (10:20 Hz) and that between the alpha and gamma (10:30 Hz) oscillations was strengthened during mental arithmetic compared to active rest condition. In addition, during the maximum WM/attentional load (mental arithmetic task with 3 digits) the synchrony between the alpha and gamma oscillations was slightly but highly significantly strengthened compared with that during the moderate WM /attentional load (mental arithmetic task with 2 digits). The CF-phase synchronies both between the alpha and beta bands and those between the alpha and gamma bands were mainly observed over the right

hemispheric parietal area. Further, in contrast to the CF-phase synchrony, 1:1 synchronies in the alpha, beta, and gamma bands, displayed a large-scale task sensitive synchrony. The spatial patterns of synchrony were distinct for these individual frequency bands, supporting the idea that they underlie distinct functional roles during task performance. This study thus demonstrates prominent CF synchrony in the human cortex. Furthermore, these data support the hypothesis that CF-phase synchrony is essential in cross-spectral integration.

6.5 New vistas for alpha frequency band oscillations

The Study V is mostly based on the findings of Studies II, III, and IV. We found that strong alpha-band phase locking was correlated with the consciously perceived stimuli in Study II. In this study, changes in the alpha-bands amplitude for either the consciously perceived or unperceived stimuli

were negligible during the time period of the phase-locked activity.

The alpha-phase locking was followed by a “conventional” amplitude suppression or event-related desynchronization (ERD)—beginning at around termination of the phase-locked response. This amplitude decrease, however, was not constrained to the alpha band, but was very prominent in the beta- and gamma-frequency bands as well. Hence, these results demonstrated that alpha phase dynamics might reveal functional roles that are currently missed by studies solely based on alpha amplitude dynamics. Moreover, in this study, the median reaction times to the stimuli occurred approximately 100 ms after the phase-locked activity but in the beginning of the alpha amplitude suppression indicating that alpha amplitude suppression cannot underlie the period of active stimulus processing itself.

Our results were in line with other studies on alpha phase-dynamics of attention (Halgren et al., 2002; Henslmayr et al., 2005; Kolev et al., 1999; Mima et al., 2001; vonStein et al., 2000) and consciousness (Gail et al., 2004) that have shown the relevance of alpha oscillations in these “top-down” functions. On the other hand, the results argued against the hypothesis that alpha oscillations reflect inhibition of sensory information processing (Neuper & Pfurtscheller, 2001; Klimesch, 1996; Pfurtscheller et al., 1996; 2003; Pfurtscheller & Lopes da Silva, 1999).

Moreover, Study III showed that the best behavioral performance is equal with low and high alpha amplitude values and that highest detection rates of weak somatosensory stimuli are obtained when the stimuli are preceded by intermediate amplitude prestimulus oscillations. These data, as well as the data of Study II, demonstrates

that the relevance of amplitude changes are extremely difficult to interpret in terms of the functional roles of the involved oscillations.

Moreover, as Study IV showed, oscillations in distinct frequency bands can be phase synchronized. This CF-phase synchrony was especially prominent between the oscillations in the alpha and beta/gamma bands. As was suggested in Study IV CF-phase synchrony might provide a mechanism for cross-spectral integration, and might therefore also provide new insights into the functional roles of the underlying oscillations. The CF synchrony between the alpha and gamma oscillations, in turn, suggests that the functional roles of these oscillations are integrated during cognitive operations.

These results together points to a direction where alpha oscillations have an active role in stimulus processing and that alpha

oscillations may be involved in the mechanism of attention and consciousness. On the hand, alpha amplitude might not reveal the functional significance of the underlying oscillation and therefore, the amplitude results thought to support “the alpha inhibition hypothesis” (Neuper & Pfurtscheller, 2001; Klimesch, 1996; Pfurtscheller et al., 1996; 2003; Pfurtscheller & Lopes da Silva, 1999) should be re-evaluated.

In this study, it is suggested that the alpha-phase dynamics as well as the CF synchrony should be taken into account in further studies examining the functional roles of the alpha band activity.

7. Discussion

7.1 Evoked vs. induced gamma-band oscillations in humans

The proposition that induced gamma oscillations in humans underlie the formation of neural object representations (Tallon-

Baudry & Bertrand, 1999) is supported by various studies showing that the amplitude and neural synchrony of these oscillations correlate with the perceptual grouping of the stimulus features as well as with perception *per se* in the human EEG and MEG (Kaiser et al., 2004; Muller et al., 2000; Tallon-Baudry et al., 1996; 1997; Rodriguez et al., 1999; Vidal et al., 2006) and in intracranial (Klopp et al., 2000; Lachaux et al., 2005, Tanji et al., 2005) recordings. In contrast, the evidence for the functional role of the evoked gamma band oscillations is, even at present, much weaker. Study I showed that auditory evoked gamma-band component is sensitive to the high-level stimulus features. This finding suggests that these oscillations might contribute to the formation of the early object representations. These early neural representations might be formed for stimuli that are perceptually unambiguous, behaviorally relevant

or well learned—possibly in early childhood (cf. Singer, 1995b). This idea is supported by more recent studies showing that also the amplitude of the auditory evoked gamma oscillations is larger for well known than for novel stimuli (Debener et al., 2003; Herrmann et al., 2004a). Herrmann et al. (2004b) suggested that the evoked gamma-band component reflects a memory match between the bottom-up and top-down information processing, whereas the induced gamma band oscillations reflect the response selection or context updating. In addition, evoked gamma oscillations have been recognized to be sensitive to task difficulty (Senkowski & Herrmann, 2002) and to reflect feature selective neural assemblies that may be top-down modulated (Busch et al., 2006a).

The familiarity of the presented stimuli modulates not only the evoked (Debener et al., 2003; Herrman et al., 2004a) but

also the amplitude of the induced response (Busch et al., 2006; Gruber et al., 2004a; 2006; Gruber & Muller, 2002; 2005; 2006). Gruber and Muller (2006) therefore suggested that these later induced gamma oscillations correspond to the activation of the cortical memory trace for the stimulus representation.

Taken together, both the evoked and induced gamma oscillations reflect high-level stimulus features and perceptual grouping (Study I; Busch et al., 2004; Kaiser et al., 2004; Keil et al., 1999; Tallon-Baudry et al., 1996; 1997), are enhanced by attention (Busch et al., 2006a; Debener et al., 2003; Fries et al., 2001b; Gruber 1999; 2002; Muller et al., 2000; Tiitinen et al., 1993;), and are modulated by memory (Gruber et al., 2001; 2004b, Gruber & Muller 2006; Debener et al., 2003; Herrmann et al., 2004a). Yet, at present, evidence indicating a role for the evoked gamma-band

oscillations in sensory object representations is insufficient to lead to general acceptance of evoked gamma oscillations contributing to the formation of neural representations.

7.2 Joint temporal and rate coding

In the locust olfactory system, temporal sequences of synchronous assemblies provide a code for olfactory sensory detection in antennal lobe networks where different odours evoke distinct spatio-temporal patterns of neuronal activity (Laurent, 1997). These dense, dynamic, and redundant representations are, however, sparsened in the areas higher in neuronal hierarchy (Perez-Orive et al., 2002) and over time (Friedrich & Laurent, 2004). An extremely sparsened coding might, in fact, be seen as reflecting the “notorious” “grand-mother cells”. An intermediate level of sparsening has, nevertheless, been suggested to help in suppressing the overlap

between the distinct neuronal representations, in limiting the interference between the distinct memories, and in facilitating the formation of the higher-level representations (Perez-Orive et al., 2002).

Indeed, Harris (2005) recently suggested that neural synchrony is only one element of the large-scale assembly formation. He suggested that the assembly formation involves sequences of synchronized cell assemblies for representing sensory stimuli or internal cognitive states and thus essentially including both the rate coding and synchrony of the neural responses. Very interestingly, in the zebrafish olfactory system rate coding signals the odour identity whereas synchrony signals the object category. These alternating coding strategies operate in different time scales (Friedrich et al., 2004).

Guyonneau et al. (2004) suggested that sparse coding is used

in the processing of visual information also. This is interesting if one considers the fact that evoked gamma-band activity is suggested to be produced by superposition of the distinct and sequential auditory middle-latency components (MLCs) occurring at intervals corresponding to gamma-band rhythmicity without no stereotypical oscillations in any of these areas (Liegeois-Chauvel et al., 1994; Yvert et al., 2001). Therefore evoked gamma oscillations might not be purely synchronized network oscillations in a classical sense, but a rhythmic evolution of local assemblies that when viewed at the macro-scale, gives rise to network oscillation. I suggest here that views on evoked gamma oscillation could be reconciled in a framework, where the evoked gamma-band component is seen to reflect the matching of the sensory stimuli to a “top-down template”. Thus, it reflects the initial feed-forward sweep of bottom-up processing as well as the

subsequent re-entrant and reciprocal re-evaluation that involved the concurrent alpha wave reflected by N1.

7.3 Early stimulus processing

Study I showed that even the evoked gamma oscillation, occurring as early as at 40-80 ms after stimulus onset, is sensitive to high-level stimulus features and might thus reflect neuronal object representations of behaviourally relevant stimuli. This is considerably earlier than the latency of the induced gamma oscillations at around 200-300 ms after stimulus onset. Study II showed that conscious and unconscious processing differs from each other as early as 30 ms after stimulus onset. Earlier studies have shown that the N1 component of event related potentials (ERP), peaking approximately at 100 ms after stimulus onset in humans, is correlated with stimulus perception both in humans (Parasuraman and

Beatty, 1980; Pins and Ffytche, 2003) and in rhesus monkey (Kulicks, 1982). In addition, also later (> 100 ms) activities of the event related response in human (Meador et al., 2002) and primate (Super et. al., 2001) primary sensory cortices are sensitive to detection. Anyhow, the cortical stimulus processing of behaviourally relevant or simple stimuli may be completed already during the early event-related response (cf. Pulvermuller et al., 1999). This is essential to the rapid behavioural responses in Study II as well as to the rapid recognition of behaviourally relevant stimuli (Asadollahi and Pulvermuller, 2001; Linkenkaer-Hansen et al., 1998; Näätänen et al., 1997; Pulvermuller et al., 2001; Thorpe et. al., 1996).

7.4 Oscillations in the prestimulus period

One of the principal findings of Study II was the divergence of conscious and unconscious sensory

processing as early as 30 ms from stimulus onset. This might, in part, be caused by neural activity in the pre-stimulus period. It has been shown that differences in the prestimulus cortical states reflecting either attention or arousal (cf. Super et al., 2003) and the anticipatory, top-down activation or priming of stimulus representations (Engel and Singer 2001; Fries et al., 2001a) may facilitate stimulus detection. In accordance with these results Study III showed that the detection probability of weak somatosensory stimuli is affected by oscillations in the prestimulus period. The detection rate was highest for the intermediate somatomotor as well as for the largest amplitude parietal alpha-band oscillatory activity. This finding may be seen as contrasting with the inhibition hypothesis, which states that large amplitude alpha oscillations should disrupt sensory detection. Nevertheless, also other studies have shown that large alpha amplitudes inhibit the

detection of sensory stimuli neither in the human visual (Thut et al., 2006) nor in the rat somatosensory (Wiest & Nicolelis, 2006) system.

7.5 Phase-locked alpha oscillations are correlated with conscious perception

Study II showed that in humans, the presence of early (~0-300 ms after stimulus onset) alpha-band phase locking was closely correlated with conscious perception. This phase locking was prominent over the cS1, cSII, and SM but also over the frontal and parietal regions, that are involved in the mechanisms of attention (Bidet-Caulet & Bertrand, 2005; Coull, 1998; Kastner & Undergleider, 2000), WM (Kaiser & Bertrand, 2003) and consciousness (Dehaene et al., 2001; Rees et al., 2002; Marois et al., 2004). Indeed, sensory awareness has been suggested to involve recurrent processing in this sensori-fronto-parietal network (Cosmelli et al., 2004; Dehaene et

al., 2007; Rees et al., 2002; see also Zeman, 2004).

In addition, our results are in accordance with previous studies using frequency-tagging methods, which showed that large-scale phase synchrony correlates with conscious perception (Cosmelli et al., 2004; Srinivasan et al., 1999; Tononi et al., 1998). Singer, Engel, and co-workers have suggested that synchrony of neuronal responses might be sufficient in supporting conscious processes (Engel et al., 1999; 2001; Engel & Singer 2001; Singer 2002). A number of studies showed that conscious perception is correlated specifically with the synchrony in the gamma band (Fries et al., 1997; Meador et al., 2002; Schurger et al., 2006). On the other hand, study of Gail et al., (2004) showed that in the monkey primary visual cortex the perception of rivalrous stimuli is correlated with the oscillations in the 4-12 Hz and 12-28 Hz bands, but not with the gamma oscillations.

In Study II, conscious perception was associated with large-scale alpha-band phase locking involving the frontal and parietal regions. Therefore these oscillations might play a central role in the system level mechanisms of conscious perception. This study also showed that conscious perception is indeed associated with early gamma-band phase locking. The gamma-band phase locking, however, was restricted to the cS1 and present only at around 100ms after stimulus onset. Therefore, it is unlikely, that this sensory cortex restricted gamma-band phase locking contributes to the actual conscious perception *per se*. Yet it is conceivable that the gamma-band phase locking reflect the formation of neuronal representation of the presented stimuli.

Consciousness has been suggested to based on a global neuronal workspace (GNW) (Dehaene et al., 2007; Dehaene & Naccache, 2001; Sergent &

Dehaene, 2004), which consists of central fronto-parietal and of more local “processors”. I suggest here, that neurons in the alpha-band synchronized sensori-fronto-parietal networks may define the “central processor” of GNW and thus underlie the system level correlate of sensory awareness.

7.6 Alpha-band phase dynamics in attention and top-down modulation

Study II underlined the importance of the oscillatory phase dynamics in the characterization of the system-level mechanisms of sensory processing. The relevance of the early phase locked alpha oscillations was also shown by an EEG study of Henslmayr (2005), which used a perceptual discrimination task and found a stronger phase locking in the alpha band in the good than bad performers in a visual discrimination task. In addition, also an early EEG study of Kolev et al., (1999) showed that alpha-band

activity phase locked to auditory stimuli in the frontal, central and parietal electrodes. The phase locking in the alpha band was enhanced in the frontal electrodes for the attended compared to that for passively listened stimuli. In this study, alpha-band phase locking was accompanied by alpha amplitude enhancement in all electrodes.

Mima et al. (2001) presented human subjects with meaningful and meaningless visual objects while recording MEG. When attended, the meaningful objects enhanced the alpha-band coherence in the occipito-temporal region, whereas the meaningless objects were followed by a decrease in the alpha-band coherence. Interestingly, these changes in coherence were not present if visual objects were passively viewed. Thus, alpha band coherence was related to object recognition.

In their seminal work, von Stein, Chiang, and König (2000) recorded neural responses from cat visual association area (A7) and A17 while the cats performed a visual GO/NO-GO task. The authors found prominent inter-areal alpha-frequency synchrony during the GO trials that was absent during the NO-GO trials. These results suggested that the alpha-band synchrony is related to the neuronal processing of behaviorally significant, expected, and top-down modulated stimuli. Even stronger support for this hypothesis were gained from phase lags in the alpha band showing that the oscillations in the A7 preceded those in A17. These results supported the idea that alpha oscillations give rise to attentional feedback modulation of the early visual processing.

In this study, the well-known and expected stimuli were occasionally interspersed with novel stimuli. In the responses to novel stimuli, the inter-areal alpha-

band synchrony disappeared and the gamma-band synchrony was slightly enhanced. In this light, the gamma-band synchrony might be related to bottom-up processing.

Taken together these studies show that alpha phase locking and synchrony are essential constituents of attention. In addition, the study of Halgren et al., (2002) and Study IV showed that alpha-band synchrony among the theta, beta and gamma band synchrony is enhanced during WM intensive mental calculation task.

The accumulating evidence on the alpha phase dynamics thus suggests that alpha oscillations are related to attention, consciousness, and WM.

7.7 Relationship between alpha-band phase dynamics and amplitude

In the alpha-frequency band, non-stimulus locked phase synchrony as well as the phase locking to stimuli do not co-vary with the alpha-band

amplitudes in a simple manner. In several reports, an enhanced alpha-band synchrony is indeed associated with an enhanced amplitude (Study IV; Gail et al., 2004; Hanslmayr, et al., 2005, Kolev et al., 1999). In Study II, on the other hand, we found strong alpha-band phase locking for the consciously perceived stimuli, and yet did not detect major alpha-amplitude changes in the time period of the phase-locked activity. Similarly, Hallgren et al., (2002) and Mima et al., (2001) found that large-scale alpha-band synchrony was, in fact, associated with simultaneous alpha amplitude suppression.

Phase interactions have been suggested to be informative in understanding the functional significance (cf. Singer, 1999; Varela et al., 2001) of neuronal oscillations, and enabling neuronal communication (Fries, 2005) as well as large-scale integration (Varela et al., 2001). Thus, alpha phase-dynamics might be seen as

appropriate means to study the functional significance of alpha-band oscillations.

In line with previous findings (Nikuline et al., 2000), Study II showed that the both perceived and unperceived somatosensory stimuli were followed by an alpha amplitude suppression. In line with the inhibition hypothesis (Klimesch, 1999; Pfurtscheller, 2001; 2003), the amplitude suppression was larger for the perceived than for the unperceived stimuli thus supporting the idea that alpha amplitude suppression reflects active stimulus processing. We, however, noted, that the amplitude suppression followed the early alpha-band phase locking (see also Vanni et al., 1997; Mima et al., 2001), and was present also in the beta and gamma bands. In this study, the behavioral responses occurred soon after the offset of alpha-phase locking (median RT ~430 ms). In this latency range, the alpha-amplitude

suppression was just beginning. These results suggest that the alpha-amplitude suppression here does not reflect the period of stimulus processing relevant to the behavioural response (*cf.* Neuper & Pfurtscheller, 2001; Klimesch, 1996; Pfurtscheller et al., 1996; 2003; Pfurtscheller & Lopes da Silva, 1999).

A useful framework in this context has been advanced by Makeig et al., (2002; 2004), who suggested that the amplitude decrease reflects a continuation of the physiological process underlying the stimulus evoked components and the phase-reset of ongoing oscillations.

7.8 Phase reset of ongoing alpha oscillations and the N1 component of the evoked responses

It is known that the N1 component of the ERP is correlated with conscious detection both in the human auditory (Parasuraman and Beatty, 1980, for a review see

Nääätänen & Picton, 1987) and visual (Pins and Ffytche, 2003) cortex. Also the corresponding component in rhesus monkey somatosensory (Kulicks, 1982) cortex is sensitive to detection. Interestingly, a body of recent data suggests that the N1 component of the ERP might arise from a phase-reset of spontaneous theta- (Klimesch et al., 2007; Makeig et al., 2002; Gruber et al., 2005) and alpha-band (Gruber et al., 2005; Klimesch et al., 2004; 2006, Hanslmayr et al., 2007; Makeig et al., 2002) oscillations. In this framework old results showing that the N1 component is correlated with attention and conscious detection are interesting as they provide additional support for the role of alpha oscillations in attention and consciousness.

7.9 Alpha band periodicity in perception

It has been shown that both humans (Broadbent & Broadbent, 1987; Chun & Potter, 1995; Potter, 1975;

1993) and rats (Uchida et al., 2003) can sample and categorize objects/odours at rates of 8-12 Hz. In addition, vanRullen et al., (2003; 2005) have shown that in a continuous-wagon-wheel illusion experiment, illusory reversals are most probable at wheel-motion frequencies around ~10 Hz. Indeed, it has been proposed that perception might operate at discrete frames of 100 ms that parallel the cycle-duration of the alpha oscillation (see Crick & Koch, 2003; vanRullen & Koch, 2003). Accordingly, it was shown that EEG alpha-band activity correlates with the perception of movement in the wagon wheel illusion paradigm (vanRullen et al., 2006).

In addition to perception, also smooth movements may be realized in discrete steps that are phase locked to the cortical alpha-band oscillations (Gross et al., 2002; Pollok et al., 2005a,b).

Thus various lines of research support the hypothesis that alpha frequency band activity underlies the discreteness of perception and movements and add on to the evidence on alphas functional role in cognition.

7.10 CF-phase synchrony

We found that CF-phase synchrony in the human cortex was very prominent in all frequency bands for frequency ratios of 1:2-1:3. During rest, the most prominent synchrony was found between the alpha and beta and between the alpha and gamma oscillations. This CF-phase synchrony was prominent in the right hemispheric parietal areas. On the other hand, the corresponding alpha, beta and gamma 1:1 synchronies were widely distributed over the cortex.

Intriguingly, the WM-intensive mental calculation task strengthened the CF-phase synchrony between the alpha and beta but especially between the

alpha and gamma bands. In addition, the harder mental calculation task, differing from the easier mental calculation task only by the number of simultaneously active neural representations in the focus of attention/WM, strengthened the CF-phase-synchrony between alpha and gamma oscillations.

These results that demonstrate the presence of task sensitive CF-phase synchrony in cortical circuits strongly support the hypothesis that CF-phase synchrony mediates cross-spectral integration. In relation to cross-spectral integration, CF-phase synchrony may enable the multiplexing of multiple simultaneously active object representations.

The finding that the CF synchronies are prominent in the right hemispheric parietal area is interesting when one considers its role in attentional functions. Imaging studies (Kastner and Ungerleider, 2000; Awh and

Jonides, 2001; Corbetta et al., 1998; Linden et al., 2003) have shown that this region is involved in WM and attention. In addition, parietal damage causes deficits especially in attentional functions (Driver and Vuilleumier, 2001; Friedman-Hill et al., 1995) or the inability to perceive multiple objects simultaneously (simultagnosia; Friedman-Hill et al., 1995). The involvement of the parietal areas in multiplexing functions is also supported by localization of cortical activity correlated with the WM capacity to the parietal regions in imaging (Linden et al., 2003) and electrophysiological (Jensen et al., 2002; Osipova et al., 2006) data.

As the alpha-band oscillations might be involved in the mechanisms of attention and consciousness, the finding of prominent CF-phase synchrony between beta/gamma and alpha-band in the parietal regions, is intriguing as further supporting the role of alpha-band oscillations in

these functions. In addition, this finding supports the possible relevance of CF-phase synchrony in mediating cross-spectral integration during attention.

1:1 synchrony may be essential in the integration of anatomically distributed processing as well as in the formation of transient neuronal assemblies (Singer, 1995; 1999; Varela et al., 2001). In addition, phase locking between and within the oscillatory assemblies permits selective neuronal communication (Fries, 2005). The finding of dynamically synchronized multi-band assemblies suggests that the CF-phase synchrony is a plausible mechanism for cross-spectral communication and thus for cross-functional integration. Recently, CF synchrony was also found between alpha and beta (Nikuline & Brismar, 2005) and between alpha and theta oscillations (Schack et al., 2005) in human EEG recordings. Obviously, many further investigations are

needed to elucidate the functions of CF-phase synchrony in neuronal networks and human cognition.

8. Conclusion

The results of the present thesis imply that neuronal processing may be extremely fast and may be completed as early as during the evoked response. In addition, alpha- and gamma- band oscillations may have parallel roles in the forming of conscious and attended object representations. It has been recognized that activity in multiple frequency bands might be required for the occurrence of a unified cognitive operations (cf. Engel et al., 2001; Engel & Singer, 2001; Thompson & Varela, 2001; Varela et al., 2001). Taken the proposed “representational” (Singer, 1999; Tallon-Baudry and Bertrand, 1999, see also Study I) and “attentional” (Study II; Halgren et al., 2002; Henslmayr et al., 2005; Kolev et al., 1999; Mima et al., 2001; vonStein et al., 2000) roles of the gamma and

alpha oscillations, respectively, I propose that neurons in the alpha-band-synchronized sensori-fronto-parietal network define the GNW, where the gamma oscillations underlie sensory object representations and thereby the “contents” of perception, WM and of the focus of attention. In this framework CF-phase synchrony underlies cross-functional integration and communication, and thereby mediates the integration of the “contents” to the fronto-parietal GNW network.

9. References

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