The top-down function of prestimulus EEG alpha activity

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"I do not know what I may appear to the world, but to myself
I seem to have been only like a boy playing on the sea shore, and diverting myself
in now and then finding a smoother pebble or a prettier shell than ordinary,
whilst the great ocean of truth lay all undiscovered before me."

\- Sir Isaac Newton (1643-1727) -

Chapter 1: Introduction

The mind[1] is the source of mental activity and now most brain scientists and even philosophers agree that mental activity arises from brain activity. Then we may ask what relation the specific brain activity has to the particular mind. For example, the brain oscillations in the alpha band (approximately 10 Hz[2]) have been known as the most dominant brain activity during relaxed wakefulness. In addition, we have our own momentary mental states in such relaxed wakefulness. Taken together, we can suppose that our momentary mental states during relaxed wakefulness would be reflected in the brain alpha activity. Therefore, in the present project, I have attempted to understand the functional dynamics of the prestimulus alpha activity and its relation to mental events from the viewpoint of top-down processing. In order to introduce the present study, general characteristics of EEG alpha activity are featured in the following section.

1.1. EEG alpha activity

The electroencephalogram (EEG) registers potential differences on the scalp that are generated by changes in underlying patterns of neural activity[3]. Electrical activity of the brain was first reported in 1875 by Richard Caton, who studied it in rabbits and monkeys (Caton, 1875; Gregory, 1998). Subsequently, Hans Berger, a German neurophysiologist, made the earliest published report describing the human EEG in 1929 (Berger, 1929). He first observed the dominant oscillations of approximately 10 Hz recorded from the human scalp in 1924 and coined the term alpha (α) frequency, using the first letter of the Greek alphabet for activity in this frequency range.

The definition of alpha rhythm[4] has been updated as the rhythm occurring at 8-13 Hz during wakefulness over the posterior regions of the head, generally with maximum

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[1] The definition of mind is still debatable, but here I refer to it as the integrated aspects of intellect and consciousness which are manifest in some compositions of perception, emotion, thought and imagination (WIKIPEDIA, 2007).

[2] The number of cycles of oscillations per second is defined as 'Hz (Hertz)'. This term is generally used for the analysis of oscillatory signals.

[3] More detailed information in regard to EEG will be discussed in Chapter 2.

[4] The term 'alpha rhythm' is most appropriately used when restricted to those rhythms that fulfill such definition. Since alpha frequency brain rhythms can be detected over other parts of the scalp than those of the official definition (i.e. occipital areas), the term 'alpha activity' is preferred to

amplitudes over the occipital areas (Deuschl and Eisen, 1999). Its amplitude varies mostly in the range of 10-50 μV in the adult. It is best observed in closed-eye subjects during physical relaxation and relative mental inactivity. It is typically blocked or attenuated by attention, especially visual, and mental effort, which is referred to as 'alpha blocking' (Berger, 1929; Adrian and Matthews, 1934; Deuschl and Eisen, 1999).

In infants, the posterior basic rhythm shows a progressive increase in frequency until it reaches a mean of approximately 8 Hz at 3 years of age and 10 Hz at 10 years of age (Niedermeyer, 1999). In unhealthy elderly people, the alpha frequency tends to decline, which apparently reflects some degree of cerebral pathology, e.g. vascular or fibrillary degeneration. However, vigorous elderly individuals may show little or no alpha frequency decline (Niedermeyer, 1999).

The origin of alpha activity

Since Study 1 (Chapter 4) and Study 2 (Chapter 5) are associated with the generation of alpha activity in relation to event-related potentials, it is worth reviewing previous studies on the origin of alpha activity. In general, the alpha rhythm is found over occipital, parietal, and posterior temporal regions (Adrian and Matthews, 1934). Since the alpha rhythm usually manifests around the posterior half of the head (i.e. most areas for processing visual information) as such, together with its blocking response to visual input, it is not surprising that the primary visual cortex has been considered as one of the sources of alpha rhythm generation (Adrian and Matthews, 1934). Since the thalamus has been suggested as playing a crucial role in the generation of cortical oscillations (Andersen and Andersson, 1968), it was tempting to assume that alpha activity is also generated by thalamic neurons. Using depth recordings on a dog, Steriade et al. (1990) proposed that thalamocortical and cortical-cortical systems interact in the generation of cortical alpha rhythm. Such a relationship between the thalamic activity and the cortical alpha rhythm has also been confirmed in human subjects by means of combining EEG and PET (Larson et al., 1998), as well as EEG and fMRI measures (Goldman et al., 2000). Consistently, on the cellular level, Hughes and Crunelli (2005) detected the gap junctions between a certain type of excitatory thalamic neurons that are capable of rhythmic firing in the alpha frequency range. They also observed that such excitatory thalamic cells exhibit a very selective connectivity and are activated by excitatory cortical input. Despite

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describe brain oscillations in the alpha frequency range. The term 'alpha activity' will be used throughout this thesis to indicate any EEG activity in the alpha frequency range, including the 'alpha rhythm' as defined here.

these various findings, the precise physiological mechanisms of alpha rhythms and their functional meaning are still little known and have to be determined in future research.

It has been proposed that there are many small independent neuronal modules in the cortex, each generating oscillations in the alpha band (Basar et al., 1997; Jones et al., 2000). Moreover, alpha-like responses have been observed in sub-cortical areas, such as the hippocampus and the reticular formation (Basar, 1999a; Schürmann et al., 2000). All of these findings have been interpreted in terms of distributed alpha systems in the brain (Basar et al., 1997). It seems that there is a complex distribution of alpha oscillations having independent sources and functional significance detectable at most parts of the scalp. The topographic distribution of alpha activity over the scalp can also vary depending on the mental activity in which a given subject is involved.

Therefore, the classical model of alpha reactivity assumes that alpha oscillations in such small modules synchronize to yield sufficient alpha activity to be detected on the scalp (DeLucchi et al., 1962; Cooper et al., 1965). Within the framework of this interpretation, so-called 'alpha blocking' is understandable as desynchronization of neuronal arrays in cortical areas involved in information processing, thus reducing alpha activity on an overlying scalp (Basar, 1980a; Pfurtscheller, 1992).

Alpha blocking

Alpha blocking in response to eye-opening was discovered by Berger on the human EEG (Berger, 1929). As shown in Figs. 1 and 8, the prominent alpha activity with closed eyes gradually disappears after eye-opening or stimulus-onset; such stimulus-induced alpha blocking was also conceived as an 'event-related EEG desynchronization (ERD)' (Pfurtscheller and Lopes da Silva, 1999). Therefore, the presence of alpha activity has been regarded as associated with a meditative, quiescent state, whereas its attenuation in the normal human has been thought to be due to attention or arousal.

There is another type of 'alpha blocking', which is derived not by visual input, but by auditory (Tiihonen et al., 1991; Lehtela et al., 1997) or higher cognitive activity (Klimesch et al., 1990; Niedermeyer, 1990, 1991, 1997). However, alpha attenuation by the non-visual modality is usually less pronounced and less consistent than the degree of alpha blocking by eye-opening (Niedermeyer, 1997). This is plausible because approximately one third of the human brain is concerned with visual processing (Celesia et al., 1996). Ellingson (1956) consistently suggested that the alpha rhythm was more closely related to visual processes than to other sensory processes.

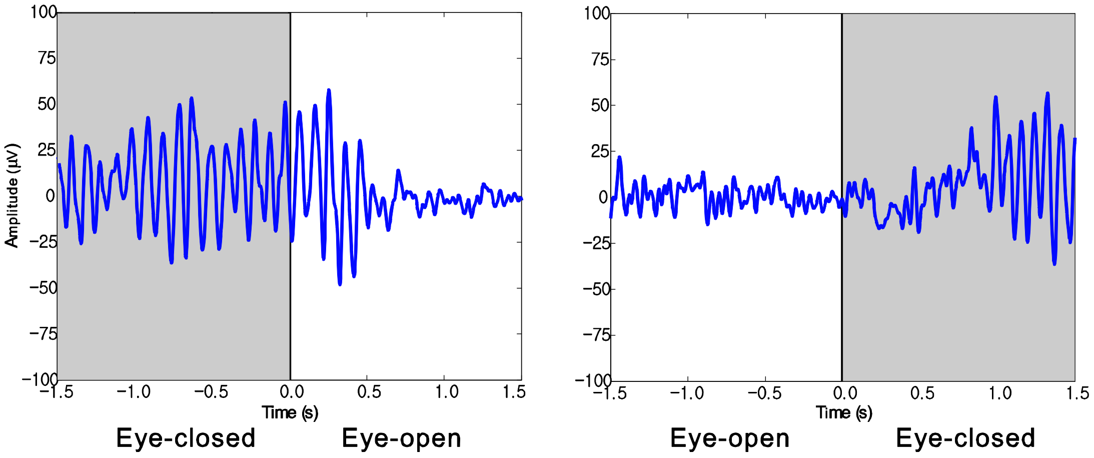

Figure 1. The brain's alpha rhythm and its blocking during eye-opening are shown in two single trials of alpha bandpass-filtered data.

There are several possible ways proposed to explain alpha blocking. The simple way is that neuronal subsets generating alpha rhythm cease to oscillate (Adrian, 1944). The other way is that the size of the oscillating array decreases and thus the signal amplitude becomes too small to be detected on the scalp. The other possibility, mentioned briefly earlier, is that information processing may disrupt synchronous alpha oscillations which were well-established before stimulation, resulting in many smaller arrays (so-called 'desynchronization'; Coenen et al., 1998). Then the resultant smaller arrays produce a smaller amplitude than when they were synchronous, since quite a large area of cortical neurons must be synchronously active for measuring the alpha activity on the scalp (Cooper et al., 1965). This argumentation is in line with a variety of evidences (Basar, 1980a; Pfurtscheller, 1992; Coenen et al., 1998).

Researchers have questioned what may interrupt such well-established spontaneous alpha oscillations in relaxed wakefulness. Some researchers have proposed that visual attentiveness (Pollen and Trachtenberg, 1972) or afferent visual input (Chapman et al., 1970) is responsible for alpha blocking. It has also been suggested that alpha activity is blocked not by visual stimulation, but by attention to stimulation, because the alpha activity reduced when the eyes are open and directed to the origin of an auditory stimulus even in the dark (Goodman, 1976). In favor of this result, other researchers (Mulholland and Evans, 1965; Mulholland and Peper, 1971) have proposed that alpha blocking is not due to 'visual attention' but to oculomotor processes such as fixation, lens accommodation, and pursuit tracking. Mulholland's group thought that extreme upward gaze tends to facilitate the posterior alpha rhythm.

Wertheim (1974; 1981) postulated that alpha activity is desynchronized during attentive, but not intentive, oculomotor behavior, irrespective of visual information processing. On the other hand, Lehtonen and Lehtinen (1972) suggested that the visual system in the waking state seems to have two modes of functioning: ocular fixation and detailed visual scrutiny. Both modes, they proposed, are likely associated with alpha blocking. They argued that attention alone is not the primary factor determining alpha blocking and that the efferent oculomotor control function is also an important parameter of occipital alpha reactivity, since vision involves oculomotor activity.

Although alpha blocking is the typical resultant phenomenon following stimulation, there are paradoxical cases of alpha amplitudes increasing even after stimulation (Klimesch, 1999; Suffczynski et al., 2001; Jensen et al., 2002; Schack and Klimesch, 2002; Busch and Herrmann, 2003; Cooper et al., 2003; Herrmann et al., 2004c; Sauseng et al., 2005a). These exceptional cases lead researchers to investigate plausible accounts for the generalized function of alpha activity. This topic will be further discussed in Chapters 6 and 7.

Intra-individual variability

It is noteworthy that the EEG data from the same individual varies from day to day, and during the same day (Kellaway, 1990). The variance of a fluctuating signal and the degree of consistency of the amplitude is referred to as stationarity. It is considerably important to establish over what period of time an EEG signal is stationary or variable. There is significant variation in the form of an individual's EEG depending on the subject's state of alertness (Lindsley, 1960; Makeig and Inlow, 1993; Makeig and Jung, 1995). The concept of level of an individual's alertness is defined by the term 'arousal'. EEG studies of arousal have shown that the alpha amplitude is highest during a relaxed attentiveness stage and declines when the subject becomes either drowsy or more aroused (so-called 'Inverted-U' model; Lindsley, 1960; Ota et al., 1996). In fact, a major source of such variation in an individual's alpha rhythm is the state of arousal or attention (Kawabata, 1974; Earle, 1988).

Attention relates to our ability to concentrate on a particular intrinsic mental activity or on a particular extrinsic stimulus of interest. As already mentioned, Berger's model of alpha blocking (Berger, 1929) stressed the fact that the alpha rhythm tended to disappear by the increased attention of the subject. However, as noted before, it is also documented that some conditions of apparently increased attention are accompanied by either no change in alpha, or even a paradoxical increase; as Adrian and Matthews (1934) noted, "a great deal can go on in the subject's brain and mind without upsetting the rhythm". This question will be further discussed in Section 1.3 and in Chapters 4 and 7.

Inter-individual variability

In addition to intra-individual variability as reviewed above, there is inter-individual variability in the characteristics of alpha activity. Davis and Davis (1936) reported that different subjects show different patterns of activity, but each reproduces his own characteristics. Golla et al. (1943), for example, classified alpha rhythms into three types according to alpha responsiveness: M (minus), R (responsive), and P (persistent) types[5]. The 'M type' alpha rhythm was extremely weak (below 10 μV), such that the effect of opening and closing the eyes or of any such stimulus was hardly visible on the record. In contrast, the 'R type' alpha rhythm represents a clearly visible rhythm (approximately 10-50 μV) during relaxed wakefulness with closed eyes and also shows alpha blocking on eye-opening or mental exertion. In the last category, the 'P type' alpha rhythm is of average size and present to an equal extent at all times, irrespective of the degree of mental activity or eye-opening. To provide a plausible explanation for such variations in alpha responsiveness, Short (1953) proposed the likely importance of a relation between alpha responsiveness and imagery types. He found that individuals with the M type EEGs used principally visual images, whereas those of the P type used verbal-motor images.

Subjects' individual alpha activity attributes have also been studied by examining cognitive performance relative to individual human intelligence (Jausovec and Jausovec, 2000; Grabner et al., 2004; Doppelmayr et al., 2005a; Doppelmayr et al., 2005b). These studies commonly reported a significant relationship between event-related changes in the alpha band and individual intelligence. This implies that the characteristics of subjects' individual alpha activity appear to reflect their individual ability for cognition and, subsequently, appear to be associated with the efficiency of their own working memory.

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[5] Similarly, Walter and Walter (1949) observed different patterns of alpha activity after eye-closing according to the features of spontaneous (or resting) alpha activity, and subsequently categorized subjects into three types: those with (a) little or no alpha rhythm, even when relaxed with eyes closed; (b) alpha rhythm easily blocked by eye-opening and mental activity; and (c) a persistent alpha rhythm, even with eyes open and when involved in mental activity.

Another example of inter-individual variability in alpha activity relates to inter-individual differences across subjects' own alpha frequencies. Klimesch's group introduced the notion of 'individual alpha frequency (IAF)' for representing such individual characteristics of alpha frequency[6] (Klimesch, 1996, 1997; Doppelmayr et al., 1998b; Klimesch, 1999). The IAF is a peak frequency of the alpha spectrum for an individual subject. Moreover, there is a tendency in alpha rhythm studies to divide the alpha frequency band into two (or three) sub-bands, each having different functional reactivity (Mecklinger et al., 1992; Cantero et al., 1999). For instance, Klimesch determined the three sub-bands for each individual subject from their IAF: 'lower 1 alpha (IAF-4 to IAF-2 Hz)'; 'lower 2 alpha (IAF-2 to IAF Hz)'; 'upper alpha (IAF to IAF+2 Hz)'. He proposed that the lower alpha band reflects attentional processes (lower 1: alertness; lower 2: expectancy) whereas the upper alpha band reflects stimulus related cognitive processes such as semantic processing (Klimesch, 1997; Klimesch et al., 1998).

In this dissertation project, I used IAFs and the amount of prestimulus alpha amplitude (cf. Chapter 4) as inter-individual variances, and compared different alpha dynamics between groups according to these inter-individual variances. I also introduced 'prestimulus alpha dominance' as an inter-individual variability in the alpha activity. This issue will be discussed further in Chapter 5.

1.2. ERP-generation and prestimulus alpha activity

In the present thesis, the relationship between prestimulus alpha activity and event-related potentials will be discussed. To get more understanding about the following studies addressing this relationship, the current issue related to the generation of event-related potentials will be briefly reviewed here.

Psychophysiologists are often interested in the EEG signals that accompany certain psychological events. These EEG waves that accompany certain events are generally referred to as 'event-related potentials (ERPs)[7]', which are one of the most frequently employed measures of the brain's electrical activity. In order to understand ERP-

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[6] They introduced IAF to get information about the shape of the spectrum of alpha frequency, and to overcome difficulties in detecting the alpha frequency of greatest power when alpha blocking occurs.

[7] This measure is discussed further in Section 2.1.1.

generation, two alternative (but not necessarily exclusive) mechanisms have been proposed (cf. Fig. 2). On the one hand it has been proposed that sensory stimulation drives random-phase ongoing EEG rhythms in each trial to partially reorganize in a coupled and coherent manner (but no other neural response additional to background activity; so-called 'phase-reset model'), and averaging these phase-coherent rhythms produces the ERP (Sayers et al., 1974; Basar, 1980b; Brandt et al., 1991; Makeig et al., 2002; Jansen et al., 2003). The alternative view suggests that stimulation may systematically elicit a neural population response with fixed polarity and latency in each trial which is added to and independent of ongoing activity (so-called 'additive power model'[8]) and that averaging these transiently coherent evoked responses across trials also results in the ERP (Jervis et al., 1983; Schroeder et al., 1995; Lopes da Silva, 1999).

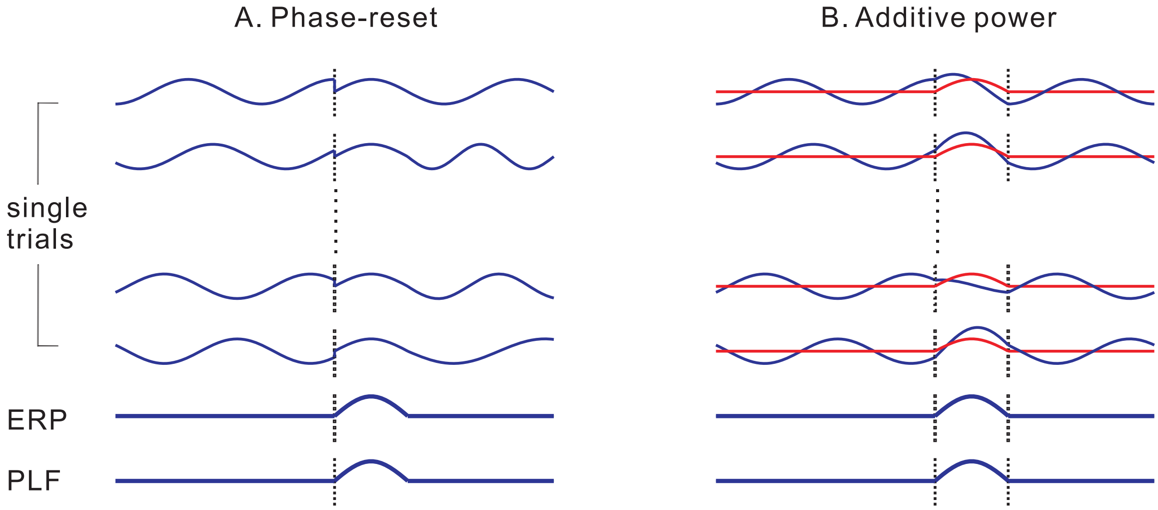

Figure 2. A schematic illustration of both models for ERP-generation; a phase-resetting model and an additive power model. In the phase-resetting model (A), stimulation induces a phase-reset (at dotted lines) and consequently results in ERP-generation. In the additive power model (B), the other averaged oscillations except 'evoked additive portion' (indicated by red dotted lines) are cancelled out in ERPs by their random phases. Importantly, phase-locking factor (PLF) cannot differentiate these two models.

By definition, ERPs are derived by averaging the poststimulus EEG activity over a sufficient number of trials. In such signal averaging, the randomness of spontaneous background EEG has to be assumed, because the main idea of 'signal averaging' is that the average response evoked by stimulation becomes more apparent as the random background EEG is canceled out by the averaging. However, there is growing evidence

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[8] This model is also referred to as evoked model in the literature (e.g. Fell et al., 2004; Klimesch et al., 2004a; Hanslmayr et al., 2007).

for arguing that the ongoing EEG activity is not simply random noise (Taylor, 1981; Basar et al., 1997). Consequently, the generation of ERPs is still a debatable issue not only because of the gap between electrophysiological observations at the scalp and the underlying neurophysiological processes, but also because of the ignorance of the potential significance of ongoing EEG activity during signal averaging.

Thus, whether the ongoing EEG activity influences ERP-generation or not has been one of the issues in ERP-generation, since the additive power model regards such an ongoing activity as a background noise, whereas the phase-reset model does not. Therefore, it has been questioned whether the ongoing EEG activity is involved in ERP-generation by means of poststimulus reorganization (i.e. phase-resetting).

As considered in the previous section, it is noteworthy that the occipital alpha oscillations characteristically demonstrate a dominant and sufficient amount of ongoing activity in relaxed wakefulness. I supposed that such prominent alpha activity in the prestimulus period is one of the favorable conditions for testing this debate in ERP-generation, because it has been suggested that phase-reorganization of ongoing activity requires a significant level of activity in the prestimulus baseline (Shah et al., 2004).

Besides, most sensory stimulation can elicit bursts of alpha activity (Basar et al., 1997; Brandt, 1997; Schürmann et al., 1997), and such bursts of alpha oscillations are not due to an amplitude increase, since the amplitude of alpha activity is generally reduced after stimulation (i.e. alpha blocking). Moreover, the amount of alpha blocking depends upon the prestimulus alpha power (Doppelmayr et al., 1998a). Taken together, I hypothesized that it is possible to differentiate between the two ERP-generation models under certain conditions, by means of the characteristic poststimulus dynamics of alpha activity, which is categorized by the amount of prestimulus alpha activity. For example, if the alpha power remained constant after stimulation but phase-locking increased compared to the baseline this would indicate phase-resetting.

Therefore, in Study 1 (Chapter 4), I categorized subjects into three groups based on the amount of prestimulus alpha activity and investigated this issue. In Study 2 (Chapter 5), in order to get more conclusive evidence for phase-resetting, I attempted to investigate the relationship between the prestimulus alpha dominance and the early ERP components. I assumed that differences in such a unique attribute as ‘dominance’ of prestimulus alpha should be reflected in the modulation of early ERP components if ongoing alpha activity is reorganized by stimulation.

1.3. Top-down processing and prestimulus alpha activity

With regard to Study 3 (Chapter 6), here I would like to introduce some fundamental information about top-down processing. When people identify an object, they have to match what they sense against their prior knowledge. Generally, there are two ways of information processing by which people accomplish their recognition: *top-down* and *bottom-up* (cf. Fig. 3).

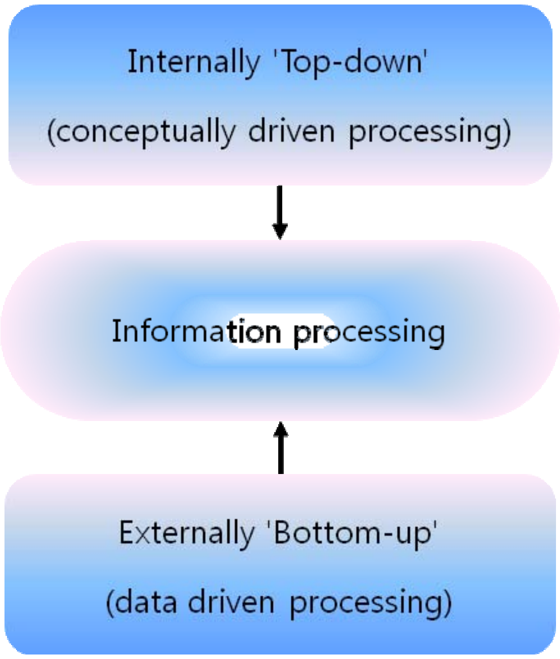

Figure 3. This diagram outlines the recognition processes that yield the transformation of incoming information at the stages of perceptual organization. Bottom-up processing (e.g. sensation) occurs when the perceptual representation is induced by the sensory input information, whereas top-down processing (e.g. identification) occurs when the perceptual representation is influenced by some higher mental functions such as prior knowledge, motivation or expectation.

Top-down processing (also called ‘conceptually driven processing’) is contingent not on the physical attributes of presented stimuli, but on information already stored in an individual’s own knowledge or memory. Especially, reasonable assumptions or common motivations about the material being processed are used for top-down constraints. That is, people make a supposition based on their established knowledge and past experience about what an object might be and then use sensory evidence to reinforce or disconfirm the supposition and to make reasonable inferences or consistent interpretations about what is really going on. On the other hand, bottom-up processing is initiated and guided by input information, and is thus called 'data-driven processing'. This occurs automatically and is pre-attentive processing, without any recourse to the prior knowledge or memory. Therefore, compared with a bottom-up fashion, a top-down approach provides a 'subjective' contribution to our everyday perception (Zimbardo and Gerrig, 2002).

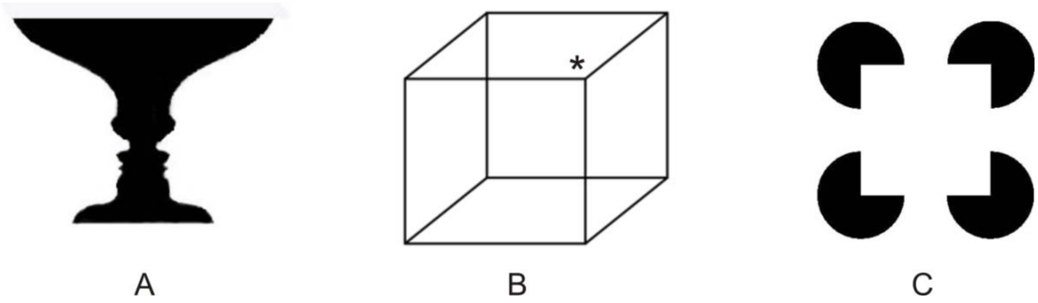

Figure 4. The first two figures demonstrate different perceptions depending on a viewer's intention. (A) a reversible goblet: its appearance alternates between a goblet and a pair of facial profiles in silhouette. (B) a Necker cube: the figure alternates spontaneously between two perspectives of the cube with respect to the asterisk-marked apex. Additionally, (C) a Kanizsa square exemplifies top-down completion from incomplete bottom-up data; there is actually no physical connection between the adjacent segments, but one may draw subjective contours between them to complete a perception of an imaginary square.

A representative example for illustrating top-down processing is the phenomenon of reversal in an ambiguous figure, which oscillates between different interpretations. For example, there are two competing aspects in Fig. 4A (so-called 'reversible goblet' or 'Rubin's vase'). The vase/faces can be seen as either a central black vase on a white background or as two opposing white faces with a black area between them; this is a kind of figure-ground reversal. Although it is perceived as the same physical shape in both interpretations, we have two different perceptions of the same objects, the perception of which appears to oscillate or flip voluntarily between the two alternatives. Thus, if people conceive one of these aspects just before looking at such a reversible figure, then they will perceive that figure as what they have conceived immediately before stimulus onset. Likewise, a Necker cube (cf. Fig. 4B) can be seen as the asterisk-marked apex of this three-dimensional hollow cube located either in front of or behind the other remaining apexes. With both examples (vase and cube), two valid interpretations alternatively flip back and forth, both however resulting from the same stimulus image (Zimbardo and Gerrig, 2002).

In addition, we sometimes have incomplete information coming into our sensory systems. To infer what the completion is, we have to do some amount of top-down processing in addition to the normal bottom-up processing. That is, we have to complete the information to determine the most probable conjecture that is consistent with the bottom-up information presented to our senses. Figure 4C demonstrates this 'top-down expectation': people perceive without doubt a white square located at the center of the figure, although no such square physically exists. In sum, both manipulation of ambiguity and expectancy of incomplete information are all dependent on one's intentional use.

As outlined above, it seems that top-down control is more relevant in tasks with internal processing demands as compared to the processing of sensory information which is primarily guided by automatic bottom-up processing. It is noteworthy that it has been reported that EEG alpha activity should be larger for the former than the latter task type. For example, Ray and Cole (1985) and Cooper et al. (2003; 2006) found smaller amplitudes of alpha activity in response to external stimuli as compared with conditions requiring internal mental processing. They interpreted differences in alpha activity in terms of internally directed or externally directed attention.

On the other hand, Shaw (1996) introduced a categorization separating 'intention[9]' from 'attention', and suggested that alpha enhancement relates more generally to the intention component. He also adopted this idea to account for a paradoxical alpha increase in conditions of apparently increased attention. Attention is associated with the selection of the organism's input, most of which is perception, whereas intention is related to the selection of the organism's output, most of which is action. In this sense, intention initiates a plan of action and controls it. For example, the central mu rhythm (at 12 Hz) is blocked by the finger movement, while the occipital alpha activity (at 10 Hz) is actually enhanced (Pfurtscheller, 1992). Even in the relationship between the oculomotor function and alpha activity, Wertheim (1974) raised a potential correlation of alpha activity with 'intention', which controls the oculomotor system by means of feedback from memory functions.

Intention can be defined as involving cognitive processes that precede any action, whether or not it involves motor activity (Brand, 1984). If we extend the realm of the meaning of intention as such, a top-down intentional component can indicate not only a

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[9] To a considerable extent, both 'intention' and 'internally directed attention', resulting in enhanced alpha, have a common aspect which is an internal concentration that they are all generated in a top-down manner.

mental preparatory state for a real movement, but also a subject's active mental attitude to process upcoming information by his own intention. For example, in order to facilitate perceptual identification, one may use intentional expectancy of what an upcoming stimulus will be. Accordingly, early perception of a stimulus can be accompanied by a kind of intention such as expectancy, and thus is embedded in a top-down process. Bottom-up sensory processing is then guided by such top-down processing as a specific expectancy (e.g. type of stimuli or task to perform). As a result, through top-down intentional processing, one can speed up perceptual identification and make it more accurate.

Interestingly, EEG alpha activity[10] has been proposed as reflecting such 'top-down expectation' (Klimesch et al., 1998; Klimesch, 1999; Babiloni et al., 2006a). Klimesch et al. (2007) suggested a top-down process in the sense that a learned memory trace is used for the encoding of an expected stimulus, and that alpha activity is associated with the semantic encoding of familiar stimuli. Further corroborating this view, von Stein et al. (2000) observed that non-stimulus-locked alpha-band neural synchrony in the cat cortex was prominent in the responses to expected objects but not in those to novel objects, which also supported a role for alpha-band synchrony in top-down modulation. They also suggested that traveling alpha waves may reflect a spread of cortical activation in the sense that one brain region controls the other region in a top-down manner. In line with this, Sauseng et al. (2005a) reported that the alpha activity in the anterior brain areas controls posterior cortical activation during top-down processing in a visuospatial task.

Then, among all frequency bands, why is the alpha activity the most possible carrier of top-down information, particularly in the prestimulus period? I would like to demonstrate the following points accounting for this conjecture.

First of all, compared with the other frequency bands, the human EEG alpha band around parieto-occipital region characteristically shows dominance and higher power either in spontaneous or in prestimulus period (Adrian and Matthews, 1934; Niedermeyer, 1999). The other oscillations, except alpha, normally do not show sufficient prestimulus activity to adequately explain the conveyance of top-down information. Thus, alpha activity most likely reflects ongoing top-down processing, which exists even before stimulus onset.

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[10] To be exact, this is the 'lower 2 alpha' according to their alpha classification (refer to Section 1.1.).

Secondly, an attribute ‘dominance’ of prestimulus alpha is a favorable condition accounting for the phase-reset model, which allows us to appreciate the functional importance of ‘ongoing’ activity probably carrying prestimulus top-down information. Then, the poststimulus reorganization of ongoing activity can be understandable within the view of an interaction between top-down and bottom-up processes. This is because in the phase-reset model stimulation influences and subsequently reorganizes prestimulus ongoing activity which may reflect top-down information. Incidentally, in contrast to other frequency bands, the alpha activity characteristically presents such dominant ongoing activity prior to stimulation.

Thirdly, only the alpha activity shows both event-related desynchronization (ERD) and event-related synchronization (ERS) after stimulation (Pfurtscheller, 1992; 2001). Although it is not yet clearly understood exactly which condition of task-performance or stimulation produces either ERD or ERS, the ERS/ERD technique detects changes in the ongoing background activity, because the poststimulus power in the filtered band is averaged and then it is compared against the prestimulus one (Pfurtscheller and Aranibar, 1977). Since the alpha activity reflects such event-related changes in ongoing activity in both directions (i.e. ERS/ERD), the alpha activity can have more capacity to reflect information of a poststimulus ongoing interaction between top-down and bottom-up processes.

In spite of the above inferences and a number of previous studies, the conclusive function of EEG alpha activity in relation to top-down processing still remains unclear and needs further investigation. This, therefore, is the context for this dissertation project. This topic will be further discussed in Chapters 6 and 7.

Chapter 2: General Methods

2.1. Electroencephalography

As mentioned earlier, the 'electroencephalogram (EEG)' is a whole measure of the electrical activity of the brain. It is recorded by means of multiple electrodes through a device called an 'electroencephalograph (EEG machine)', and the technique is referred to as 'electroencephalography'. The changes in electrical potential recorded on the scalp are produced generally by the sum of the excitatory and inhibitory postsynaptic potentials (EPSPs and IPSPs) of the cortical neurons (especially, pyramidal cells). The neurons transmitting electric signals to their synapses act as electromagnetic dipoles that constitute intracortical generators of the EEG.

To make such substantial signals that are detectable on the scalp, the source dipoles should be oriented in a certain direction. Fortunately, cortical pyramidal cells are mostly arranged in parallel to one another and most cortical functions are associated not with a single neuron, but with synchronized neuronal assemblies. When quite a number of neurons are simultaneously activated with a unidirectional orientation, these result in measurable signals in the form of EEG. Therefore, such well-synchronized electrical dipoles of neuronal subsets are measurable even on the scalp. Since brain potentials varying over time do not usually measure more than 100 μV, such tiny signals need to be amplified for more detailed investigation. Thus each electrode is connected to a powerful amplifier and registered for further analyses.

Furthermore, multiple channels allow investigators to record EEG activity simultaneously from different scalp sites. Electrodes are placed in a certain standardized manner. For example, the international 10-20 system (Jasper, 1958) uses 10% or 20% of specified distance as the electrode interval, and the outlined distances are measured from bony landmarkers (nasion and inion). This conventional standardized system provides researchers with a consistent measuring condition over time and over place.

However, there are some restrictions in the EEG measurement. If the source has a so-called 'closed field' structure, in which the sum of each dipole's power mostly cancels out by dipoles' random orientations, the signal will not be strong enough to be detected from a far-distance (Proverbio and Zani, 2002). In addition, the scalp EEG signal reflects the sum of electrical activity arising in a large volume of the brain; not only EPSPs/IPSPs, but also action potentials and electrical signals from the skin, muscles, blood, and eyes. Thus the utility of the scalp EEG is unable to provide a disentangled view of neural activity, which we definitely want to investigate.

In this respect, electroencephalography initially fails on spatial resolution, in spite of its high temporal resolution (approx. millisecond scale). Although some source-localizing methods are developed to complement such a lower spatial resolution (Koles et al., 1995; Koles and Soong, 1998; Sclabassi et al., 2001; Srinivasan et al., 2006), the reliability of these methods is still controversial due to so-called 'inverse-problem'; any given surface distribution of electrical activity can be explained by an infinite number of intracranial neural source distributions that produce an identical surface map. Accordingly, one can roughly estimate the source of a signal of interest through such methods. Otherwise, researchers are favorable to co-register such neuroimaging techniques with relative high-spatial resolution as 'functional magnetic resonance imaging (fMRI)' or 'positron emission tomography (PET)'. In the co-registration method, the amplitude of EEG signals recorded on the scalp is color-coded and plotted on the surface of three-dimensional MRI scan (Gevins et al., 1995).

2.1.1. Analysis in the *time* domain: event-related potentials

When one is interested in a time series of event-related changes in EEG, one focuses on examining how the waveforms recorded at individual electrode sites vary over time across one or more experimental conditions. This is an analysis of event-related potentials (ERPs), which are computed from averaging the poststimulus EEG over a sufficient number of trials, as mentioned in Chapter 1 (cf. Fig. 2). ERPs are based on the electrophysiological recording of brain potentials synchronized with the presentation of external sensory stimuli (so-called 'exogenous') as well as the occurrence of internal cognitive events (so-called 'endogenous'; Donchin, 1979; Hillyard and Kutas, 1983; Picton and Hillyard, 1988). In general, ERPs are wave-forms characterized by a series of positive or negative deflections. Such ERP components are commonly denoted by their relative polarity (positive, P; negative, N) followed by the number of milliseconds of their approximate latency, e.g. P100, N170, P300 and so on (Proverbio and Zani, 2002).

The characteristics of specific ERP components, such as amplitude and latency, are quantified as a function of the specific experimental condition. The early ERP components are more strongly influenced by bottom-up (sensory or physical) factors than are the later components, which reflect higher cognitive processing. For example, visual P1(00) is more subject to physical aspects of stimuli (Skrandies, 1984; Zani and Proverbio, 1995), whereas P3(00) has been known in relation to top-down processes such as stimulus-evaluation or context-update (Kutas et al., 1977; Donchin and Coles, 1988; Ravden and Polich, 1998). However, it seems that the higher mental processing is not restricted only to late 'cognitive' ERP components. For example, brain activity at early latencies (corresponding to the P1) is affected by the semantic meaning of the stimuli (Skrandies, 1998). These observations show how visually evoked brain activity is modulated by the meaning of the stimuli at the early stage of information processing. P1 is thus probably modulated not only by external stimulus property, but also by internal mental conditions[11].

Although the ERPs are able to provide very precise temporal information on the time course of the various processing stages, ERP analysis involves critical assumptions, one of which is the ignorance of the significance of ongoing brain activity. That is, the background activity is regarded as noise, which should be cancelled out by signal averaging. In addition, trial-based variances are ignored in the analysis of ERPs. Thus, the dependency or independence of ongoing activity is crucial for understanding what really occurs after stimulation, some of which is relevant to the investigations reported here.

2.1.2. Analysis in the *frequency* domain: event-related oscillations

In addition to the EEG analysis in the time domain, the EEG measures can be investigated in the frequency domain. Moreover, it has been demonstrated that spectral analyses can often yield significant insight into the functional cognitive correlations of the signals (Basar et al., 1999; Freeman, 2000; Basar et al., 2001). As described earlier, Berger (1929) first observed the dominant oscillations of approximately 10 Hz recorded from the human scalp and named it alpha rhythm. He also found the second type of oscillatory activity that is called beta activity (approximately 13-30 Hz), and Jasper and Andrews (1938) labeled high-frequency oscillations at 35-45 Hz as gamma waves (nowadays, conventionally 30-80 Hz). The slow oscillations below 4 Hz and approximately 4-8 Hz were referred to as delta and theta waves, respectively. Although the frequency range of the EEG has a fuzzy boundary, such a categorization as shown in Table 1 is commonly used (Niedermeyer, 1999).

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[11] In Chapter 5, I have thus attempted to investigate whether such an early ERP component as P1 is subject to the 'ongoing' brain activity which may reflect a mental state prior to stimulation and influence subsequent information processes.

Table 1. A list of categories of oscillatory activity. The Greek letters alpha, beta, delta, theta and gamma are commonly used for the different wave frequencies apparent in the EEG. For instance, alpha activity stands for brain waves with a periodicity of about 8 to 13 per second.

Frequency	Name
Below 4 Hz	Delta (δ)
4-8 Hz	Theta (θ)
8-13 Hz	Alpha (α)
13-30 Hz	Beta (β)
Above 30 Hz	Gamma (γ)

As the features of alpha activity have already been reviewed in Chapter 1, those of the other oscillatory activity will be briefly considered here. Oscillations occurring around the delta frequency usually relate to deep sleep (Steriade et al., 1993). Delta activity is generated either in the cortex or in the thalamus (Steriade, 1999), and corticothalamic connections are capable of synchronizing delta-oscillating thalamic neurons that were uncoupled before cortical stimulation (Steriade et al., 1991). Delta and theta activity account for the slow potentials in ERPs, such as P3, N4, and so on (Basar-Eroglu et al., 1992). Event-related theta activity has been considered with working memory functions (Klimesch, 1999; Jensen and Tesche, 2002). Moreover, theta activity associated with memory performance has been reported as interacting with the gamma activity (Fell et al., 2003; Demiralp et al., 2006). Gamma oscillations have been studied in relation to higher brain functions (Engel et al., 2001). The functional relevance of gamma activity has been assessed in attention (Tiitinen et al., 1993; Herrmann et al., 1999; Debener et al., 2003), binding phenomena (Tallon et al., 1995; Tallon-Baudry et al., 1996; Müller et al., 1997), memory (Herrmann et al., 2004a; Herrmann et al., 2004b) and perceiving meaningful objects (Tallon-Baudry et al., 1997; Keil et al., 1999). Additionally, beta waves have been investigated in the context of movement; beta activity is suppressed during movement (Neuper and Pfurtscheller, 2001), and it is observed even during imagined movements (Salmelin and Hari, 1994). Beta oscillations have also been reported in relation to cognitive processes such as memory rehearsal (Tallon-Baudry et al., 2001).

Oscillations are characterized by their amplitude, phase, wavelength and frequency. The phase means the angular position of the vector-revolution within a cycle of a periodic waveform. The phase of an EEG oscillation is from 0 to 2π. The wavelength stands for the distance between repeating units of a wave pattern, and has an inverse relationship to frequency, which is defined as the rate of change of phase of a sinusoidal waveform.

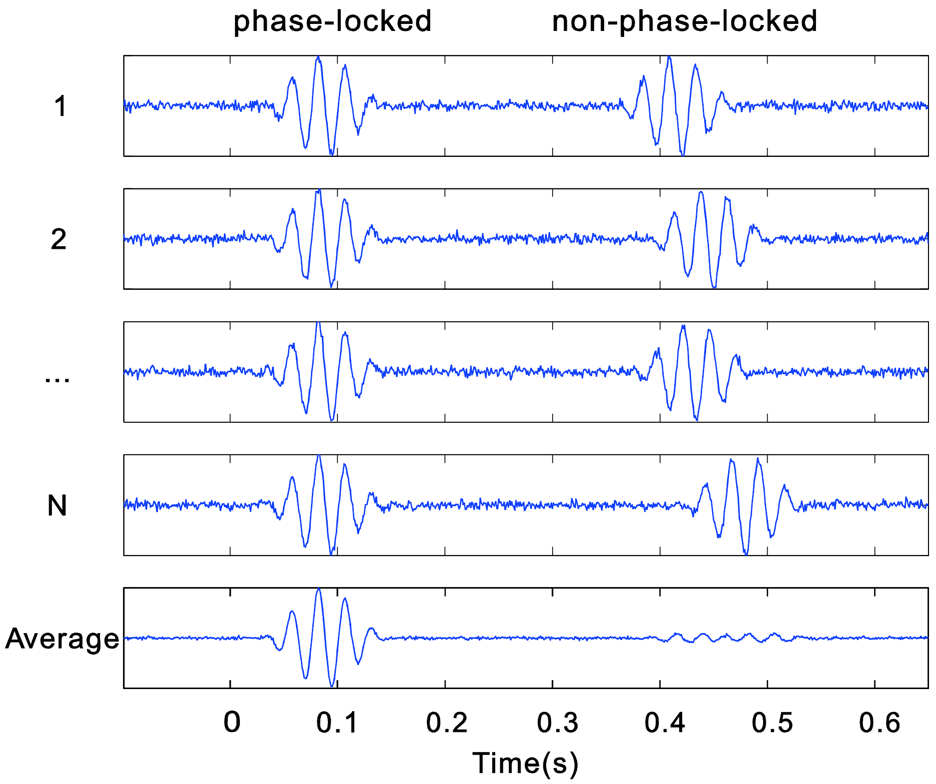

Figure 5. When oscillations occur at the same latency and with the same phase in multiple trials (1 to N), the average of them results in the phase-locked (evoked) activity, as shown in the bottom row. On the other hand, if the latency or phase of oscillations in each trial jitters relative to stimulus onset, non-phase-locked (induced) activity is almost cancelled out in the average (adapted from Herrmann et al. (2004a)).

Galambos (1992) classified oscillatory activity into different types according to the degree of phase-locking to the stimulus: spontaneous, induced, and evoked rhythms[12]. In this framework, spontaneous activity is completely unrelated to the occurrence of stimulation. Induced activity is indeed correlated with experimental conditions but is not strictly phase-locked to the onset of an event, whereas evoked activity is strictly phase-locked to the onset of an event across trials (cf. Fig. 5). Evoked activity usually results from any kind of sensory events such as visual, auditory, or somatosensory stimulation, while induced activity is most commonly observed during cognitive tasks, suggesting that the non-phase-locked oscillations are produced from different cell assemblies to temporally bind different ongoing information for complete perception.

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[12] Emitted rhythms in response to omitted stimuli have also been introduced in his classification, but I will not address these here.

2.2. Wavelet analysis

In principle, every signal constitutes a mixture of multiple sinusoidal waves of various frequencies. The most common methods in decomposition of EEG signal are filtering, Fourier transformation, and wavelet analysis.

Filtering is conceptualized as removing unwanted signal components (e.g. noise activity) and thus focusing only on those desired. For example, a bandpass filter allows only a limited spectral range to pass. A digital filter works by performing mathematical operations on a digitized form of an analog signal and thus the input signal must be of limited frequency content (i.e. to avoid aliasing[13]), whereas an analog filter should rely on the attributes of electronic components in physical networks to achieve the desired filtering effect (Edgar et al., 2005).

On the other hand, Fourier analysis transforms a digitized EEG signal into a series of sine waves of varying frequency, amplitude and phase. Since Fourier transformation assumes that the derived frequency components are present over the whole duration of the analyzed signal epoch, Fourier analysis cannot provide us with anything about the time occurrence of the signal components in the resultant spectrum. To make matters worse, such an assumption of stationarity is generally violated in biological signals such as the EEG.

A number of techniques have been developed to overcome this problem. Sometimes the Short Time Fourier Transform (STFT) is used; the signal is analyzed in quite short epochs (e.g. 0.5-2 seconds) with successive epochs, which often overlap. However, this method also presents problems because there is a trade-off between a temporal resolution and a spectral resolution, inversely proportional to each other according to the 'uncertainty principle[14]'. This principle suggests that one cannot know what spectral components exist at particular instances of time with absolute precision. Instead, one can know the temporal intervals at which the spectral bands exist.

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[13] Only if a sampling is executed at least twice per cycle from the original signals, can it provide a discrete time series that accurately represents the frequency of a sine wave (Nyquist's rule). If this rule is violated, the resulting digitized waveform may contain low-frequency components that are not present in the original data, which is known as 'aliasing'.

[14] Indeed, this comes from the Heisenberg uncertainty principle, which states that position and momentum of an elementary particle cannot be simultaneously measured with arbitrary precision.

Although such a resolution problem exists even in wavelet analysis, wavelet analysis is one technique for addressing the time factor problem; the main defect of STFT is the fixed window size irrespective of the analyzed frequency, whereas wavelet analysis is optimized by applying windows of variable length, depending on the analyzed frequency. That is, by modifying the scaling factor, the corresponding wavelet transform zooms from coarser (for low-frequency) to finer (for high-frequency) signal structures. Moreover, a complex wavelet function can yield not only the amplitude, but also the phase of the signal oscillations in the analyzed frequency band, which is advantageous over the filtering method.

As depicted in Fig. 7, the mother wavelet is constructed to have a zero mean and to be localized in both time and frequency domains. Owing to this localization property, the wavelet transform provides us with temporal information of non-stationary signals, which is unfeasible in the Fourier analysis. The wavelet is first chosen to have a proper shape according to the purpose of analysis and to have a duration that is a fraction of the EEG epoch to be analyzed. The signal to be analyzed is then convolved with the wavelet at successive time points of the signal. Portions of the signal having the same spectral components as the wavelet will be detected and displayed.

To represent a wavelet transform computation in a formula expression, the original signal time series $\chi(t)$ is convolved with a scaled and translated version of a mother wavelet function $\Psi(t)$. The convolution leads to a new signal of wavelet coefficients,

$$\mathrm{W}_{\chi}^{\Psi}(a,b) = A_{\Psi} \cdot \int \Psi^{*}\left(\frac{\mathrm{t}-b}{a}\right) \cdot \chi(t)\, dt$$

where A_{Ψ} represents a (wavelet-specific) normalization parameter[15], and Ψ^* denotes the complex conjugation of the wavelet function; a is the wavelet's scaling factor, and b is the translation parameter (Herrmann et al., 2005). This equation indicates that the wavelet

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[15] In order to have unit energy at all scales, the wavelet functions should be normalized prior to the convolution; for the Morlet wavelet transform, the normalization parameter is $\sigma_t^{-1/2}\pi^{-1/4}$. If using the Gabor normalization parameter, $\sigma_t^{-1}(2/\pi)^{1/2}$, the wavelet amplitude spectrum produces the instantaneous amplitude of an activity. The main difference between the wavelet transform and the Gabor transform is that the width of the data window to be analyzed is not fixed in the wavelet method, but adapted to the frequency for the analysis.

coefficients quantify the similarity between the original signal and the applied wavelet function.

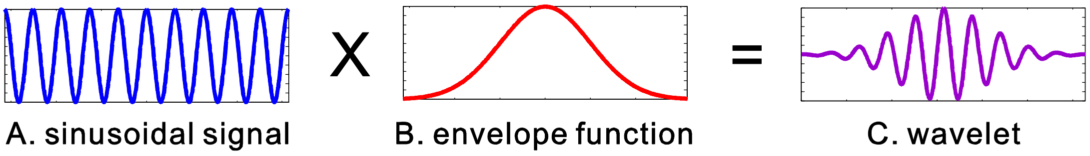

Figure 6. This figure schematically depicts an example of producing a wavelet (adapted from Herrmann et al. (2005)). Multiplying a sinusoidal signal (A) and an envelope function (B) yields a wavelet (C).

Thus, the wavelet coefficients are subject to the choice of the mother wavelet function. For detecting sinusoidal EEG signals, sinusoidal wavelets are ideal, because the wavelet transform is similar to detecting whether the signal component contains the applied wavelet component or not. For example, in the case of Morlet's wavelets, one of the sinusoidal mother wavelet functions, the formula is given as

$$\Psi(t) = \mathrm{e}^{j\omega_0 t} \cdot \mathrm{e}^{-t^2/2}$$

where j stands for the imaginary unit ($\sqrt{-1}$), and ω_0 is 2π times the frequency of the unshifted and uncompressed mother wavelet. Morlet wavelets are complex functions[16] and both real and imaginary parts consist of a harmonic oscillation windowed in time by a Gaussian envelope, as illustrated in Fig. 6.

In the frequency domain, the shape of a Morlet wavelet can be represented by its center frequency and deviation, because the Morlet wavelet has a Gaussian shape centered at the modulation frequency (cf. Fig. 7). Therefore, if a wavelet is scaled and unshifted, it is described as a function of frequency (f),

$$\Psi(t, f) = \mathrm{e}^{j2\pi f t} \cdot \mathrm{e}^{-t^2/2\sigma_t^2}$$

where σ_t denotes the standard deviation of the Gaussian temporal envelope; the standard deviation in the frequency domain is reciprocally related to that in the time domain,

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[16] A wavelet function can be considered as a finite impulse response filter; for example, the real part of the Morlet wavelet transform corresponds to a bandpass-filtered signal, while the imaginary part represents a 90-degree phase shifted signal (Hilbert transform). Then, the absolute value $|W_x(t,f)|$ indicates the envelope of the filtered signal and quantifies the instantaneous oscillatory strength of the signal with respect to the frequency band for the analysis.

$$\sigma_f = (2\pi\sigma_t)^{-1}$$

In order to obtain the wavelet's scaling properties, σ_f is proportionally related to the frequency (i.e. σ_t is reciprocally related to the frequency). This implies that the Morlet wavelet transform has a different time and frequency resolution at each scale. As the number of significant wavelet cycles is computed as $n=6\sigma_t f$, and σ_t is reciprocally related to the frequency, all frequencies have the same number of significant wavelet cycles. As such, the length of a Morlet wavelet varies in the temporal domain as a function of frequency, because the wavelets of the same number of cycles spread over a shorter interval for higher frequencies and a longer interval for lower frequencies (cf. Fig. 7). Hence, the temporal resolution of a wavelet is better at higher frequencies, whereas the frequency resolution of a wavelet is better at lower frequencies.

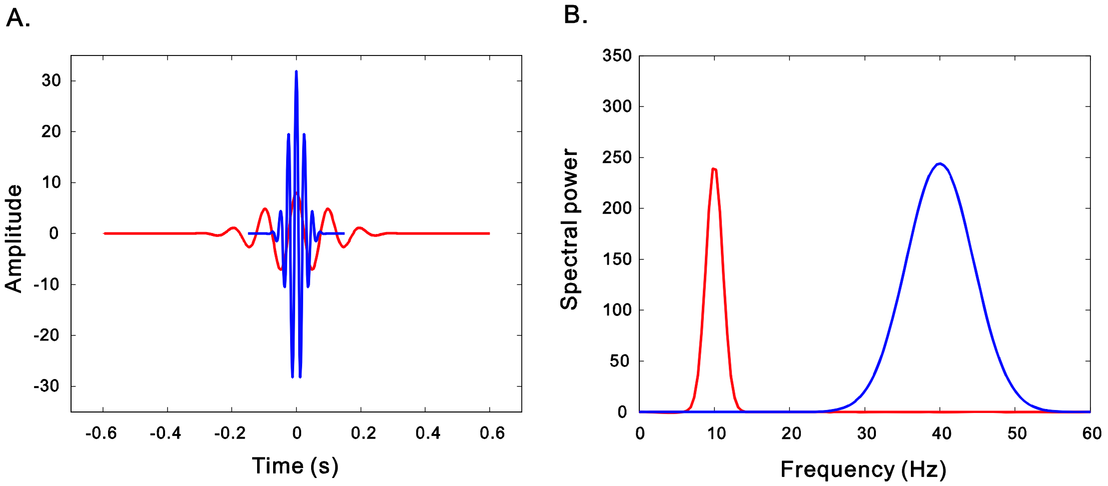


Figure 7. These figures represent two Morlet wavelets with different central frequencies in the temporal domain (A) and their corresponding spectra (B). A low-frequency wavelet of 10 Hz (red lines) shows a lower resolution (relatively broad-band) in the temporal domain in spite of a higher resolution (relatively narrow-band) in the spectral domain, whereas a high-frequency wavelet of 40 Hz (blue lines) represents a higher temporal resolution with a lower spectral resolution (adapted from Herrmann et al. (2005)).

To obtain phase-locked (evoked) activity, the wavelet transform is applied on the average over the single trials as follows:

$$\text{Evoked activity} = \left| A_\Psi \cdot \int \Psi^*\left(\frac{t-b}{a}\right) \cdot \frac{1}{N}\sum_{i=1}^{N} eeg_i(t)\, dt \right|$$

On the other hand, to calculate the activity that is not phase-locked to stimulus onset, the total activity, which consists of evoked and induced activity, can be computed as follows:

$$\text{Total activity} = \frac{1}{N}\sum_{i=1}^{N}\left|A_{\Psi} \cdot \int \Psi^{*}\left(\frac{\mathrm{t}-b}{a}\right) \cdot eeg_{i}(t)\, dt\right|$$

To avoid cancelling out non-phase-locked activity in the average, each single trial is first transformed and the absolute values are averaged subsequently. Therefore, the total activity contains all poststimulus activity, no matter whether it is phase-locked to the stimulus or not.

In order to obtain a time-frequency (TF) representation of the analyzed signal, wavelet transformation can be applied to multiple frequencies; the wavelet transformation is repeated by consecutively changing the frequency band to be analyzed. The result is an accumulative series of a time-frequency plot, representing not only the spectral component of the epoch analyzed but also the temporal component of activity within each band. As displayed in Fig. 8, the TF representation has been yielded by color-scale coding of the wavelet amplitudes with x-axis indicating a time-domain and with y-axis indicating a frequency-domain.

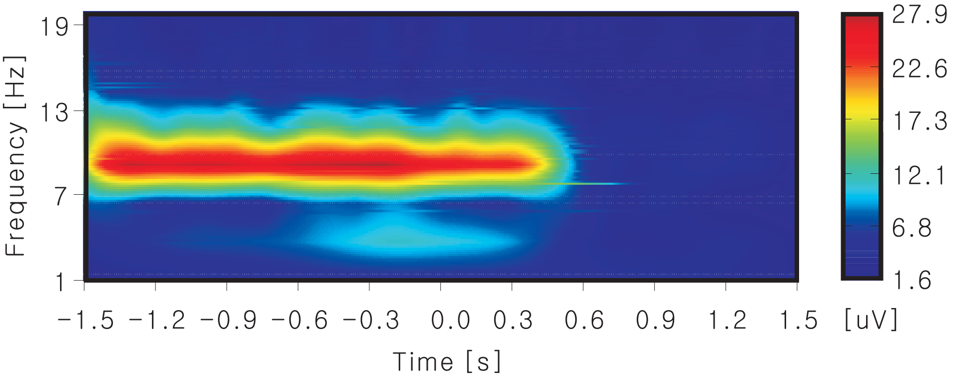


Figure 8. An example of a time-frequency representation: eye-opening (at time point zero) leads to clear alpha blocking in the total activity.

Chapter 3: Working Hypotheses and Outline of Studies

The theoretical and methodological backgrounds were reviewed in Chapters 1 and 2. In this chapter, I would like to briefly describe the working hypotheses, and how the hypotheses lead to the empirical questions pursued in the three studies. The hypotheses will be examined and explained in more detail in the following chapters.

As introduced in Chapter 1, the EEG alpha activity exhibits dominant activity around the parieto-occipital region during relaxed wakefulness. On the basis of these particular characteristics of alpha activity, the following hypotheses in relation to the prestimulus alpha activity are tested in the present project:

- *Hypothesis 1* (regarding the relation between *prestimulus alpha* and *poststimulus EEG dynamics*): I expect that both phase-resetting of EEG alpha activity and additive power contribute to ERP-generation.

As outlined in Chapter 1, there is still an ongoing debate on the two ERP-generation models: phase-reset or additive power. The dominant and sufficient prestimulus alpha activity may provide a pertinent condition for investigating whether phase-resetting contributes to ERP-generation. I supposed that it might be possible to verify the two debatable models for ERP-generation by investigating differences in poststimulus EEG alpha dynamics in terms of total and evoked activity, depending on the *amount* of prestimulus total alpha activity. This hypothesis will be tested in Study 1 (Chapter 4).

- *Hypothesis 2* (regarding the relation between *prestimulus alpha* and *poststimulus ERP dynamics*): I expect that dominance of prestimulus EEG alpha activity modulates early event-related potentials in favor of phase-resetting.

If there is considerable evidence for the dependency of poststimulus EEG dynamics on prestimulus ongoing alpha activity through Study 1, then some properties of prestimulus ongoing alpha activity should be reflected in the subsequent event-related responses as a result of their influence. Moreover, this may occur most likely at the early stage of information processing, since the characteristics of prestimulus ongoing activity for poststimulus reorganization will gradually decay after stimulus onset. Thus, the early response to stimulation may reflect more characteristics of prestimulus ongoing activity within the framework of phase-reorganization. All such results will provide substantial evidence for phase-resetting of ongoing activity after stimulation.

To assess this question in Study 2 (Chapter 5), I used an attribute 'dominance' of prestimulus alpha activity, since I assumed that ongoing activity putative for effective phase-resetting should keep its dominance until a stimulus comes to initiate reorganization of ongoing activity. Generally, the parieto-occipital alpha activity in relaxed wakefulness spontaneously shows relative dominant activity among all oscillatory activity (Adrian and Matthews, 1934; Niedermeyer, 1999). Accordingly, if ongoing alpha activity is reorganized by stimulation (i.e. phase-reset), differences in such a unique attribute as 'dominance' of prestimulus alpha should be reflected in modulation of the ERP components at the early information processing stage.

- *Hypothesis 3* (regarding the relation between *prestimulus alpha* and *its putative top-down function*): I expect that the amplitude of prestimulus alpha activity predicts poststimulus changes in event-related cognitive and behavioral responses from the viewpoint of top-down reflection.

As Klimesch et al. (2007) recently pointed out, the paradoxical enhancement of alpha activity can be noticeably observed during task-performance either under the particular conditions where subjects have to withhold task-relevant information or over the brain regions that are task-irrelevant (Klimesch, 1999; Suffczynski et al., 2001; Jensen et al., 2002; Schack and Klimesch, 2002; Busch and Herrmann, 2003; Cooper et al., 2003; Herrmann et al., 2004c; Sauseng et al., 2005a). Since these specific conditions may imply a possible top-down function in inhibiting task-irrelevant information, Klimesch et al. (2007) postulated that alpha synchronization might reflect a top-down inhibitory control.

In addition, following Study 2, if there is significant evidence for the relationship between prestimulus alpha and poststimulus ERPs within the framework of phase-resetting of ongoing alpha activity, then a prestimulus intentional mental state (or top-down processing prior to stimulation) can be reflected in the prestimulus ongoing alpha activity, and may interact with the subsequent bottom-up processing, which is probably reflected in event-related cognitive (e.g. P3 component) and behavioral (e.g. reaction time) responses.

To evaluate this hypothesis together with Klimesch's supposition of top-down inhibition (Klimesch et al., 2007), I designed two kinds of discrimination tasks, in which the two tasks required the inhibition of the task-irrelevant feature to improve task-performance. This experimental paradigm might induce different top-down inhibitory processes across the two tasks. Different salience of the two stimulus-features might also lead to different task-difficulties. Then, I supposed that both different top-down inhibitory processes and different task-difficulties prior to stimulation might be reflected in prestimulus alpha activity. Thus, I attempted to investigate any significant differences in prestimulus alpha activity in relation to different poststimulus task-performance in Study 3 (Chapter 6).

Chapter 4: Prestimulus alpha activity and EEG dynamics (Study 1)

The experimental results presented in this chapter have been published in the *International Journal of Psychophysiology* (Min et al., 2007).

4.1. Introduction

The event-related potential (ERP) is one of the most frequently employed measures of the brain's event-related electrical activity. It is derived by averaging the poststimulus electroencephalogram (EEG) over a sufficient number of trials. However, the generation of ERPs is still an issue of ongoing debate because of the gap between electrophysiological observations at the scalp and the underlying neurophysiological processes (e.g. Makeig et al., 2004). Two alternative (but not necessarily exclusive) mechanisms have been proposed. On the one hand it is assumed that stimulation induces a partial 'phase-resetting' of ongoing EEG rhythms in each trial, and averaging these phase-coherent rhythms produces the ERP (Sayers et al., 1974; Basar, 1980b; Brandt et al., 1991; Makeig et al., 2002; Jansen et al., 2003). The alternative additive ERP view suggests that stimulation elicits a neural population response with fixed polarity and latency in each trial which is additive to and independent from ongoing activity (so-called 'additive power model') and that averaging these evoked responses produces the ERP (Jervis et al., 1983; Schroeder et al., 1995; Lopes da Silva, 1999).

Although the mechanisms that are at work in the generation of the ERP have been debated and investigated for decades, researchers are still at odds on the methods which would allow one to distinguish between the 'phase-reset' and the 'additive power' models as outlined above. The consistency of the phase of oscillatory activity across trials can be quantified by means of the so-called 'phase-locking factor (PLF)' (Tallon-Baudry and Bertrand, 1999; Delorme and Makeig, 2004; Herrmann et al., 2005). Although measures of phase consistency across trials have been used to provide evidence for a stimulus induced reorganization of ongoing activity (Brandt, 1997; Jansen et al., 2003), it is important to point out that an increase in phase-locking *per se* is not informative about the generating mechanism because either phase reorganization or additive responses with fixed latency and polarity in each trial can produce an increase of inter-trial phase consistency (Jervis et al., 1983; Makeig et al., 2002; Klimesch et al., 2004b; Makeig et al., 2004; Shah et al., 2004; Yeung et al., 2004).

Therefore, for a comprehensive analysis of the event-related EEG dynamics, it appears necessary to consider both phase and amplitude dynamics. Common measures of oscillatory EEG activity comprise evoked and induced activity as well as the phase-locking factor. Evoked activity is computed as the time-frequency representation of the ERP and contains signals that are strongly phase-locked to stimulus onset. Induced activity is a measure of oscillatory power in single trials and captures signals that are not phase-locked to stimulus onset.

In former studies (Makeig et al., 2002; Klimesch et al., 2004a; Shah et al., 2004) it has been stated that a pure phase-reset of ongoing activity would be indicated by changes in evoked activity and phase locking factor without a change in signal power in single trials. This would be true if background oscillations would not exhibit modulations of amplitude to a stimulus at the same time. However, it is well known that brain oscillations show a variety of amplitude modulations according to a stimulus or task. Whereas some oscillations exhibit a decrease in power, e.g. alpha (Klimesch, 1999), others show an increase in power, e.g. theta (Basar-Eroglu and Demiralp, 2001; Debener et al., 2005) and gamma (Herrmann et al., 2004a). Thus, it appears plausible that an evoked response, superimposed on background EEG, occurs at the same time as a power decrease. This additive component might then elicit an increase in PLF with no observable power increase being visible in the EEG due to the strong simultaneous decrease. This line of argumentation was used by Klimesch et al. (2006) in order to explain why Mäkinen et al. (2005) failed to observe an influence of ongoing brain activity in ERP-generation. That is, amplitude variance alone is not sufficient to distinguishing between an additional evoked response and phase-resetting of ongoing activity. For these reasons, it is impossible to dissociate between the ‘phase-reset’ and the ‘additive power’ models by simply considering poststimulus power changes or phase-locking dynamics if alpha-blocking occurs.

However, under certain conditions, it may be possible to differentiate between the two models. If the alpha power remained constant after stimulation but phase-locking increased compared to baseline this would indicate phase-resetting (Klimesch et al., 2004a; Shah et al., 2004). Therefore, we categorized our subjects into three groups based on the amount of prestimulus alpha activity. Since the amount of ERD depends upon the prestimulus alpha power (Doppelmayr et al., 1998a), we expected to find subjects who showed no poststimulus decrease of alpha but an increase of phase-locking. While our categorization yielded interesting results, however, it did not yield a group of subjects without modulation of alpha power after stimulation as would be required for the differentiation of the two models. Thus, in addition, we applied a simulation analysis to the data of all three groups, as recently suggested by Hanslmayr et al (2007).

In the present study, we analyzed data recorded in a visual discrimination experiment in order to find evidence for one of the two models of ERP-generation. As has been pointed out by Shah et al. (2004), phase-resetting of ongoing activity requires that there be a significant level of activity in the prestimulus baseline, a requirement which is usually fulfilled for the alpha frequency range. We therefore restricted our analysis to activity in the alpha band in the present study. We reasoned that if event-related EEG signals were in fact dependent on ongoing EEG activity it would be plausible that the prestimulus brain state influences the subsequent response. Therefore we investigated differences in the event-related EEG dynamics of three subgroups of subjects, which were categorized according to the amount of prestimulus total alpha activity. Such different amounts of prestimulus alpha activity yielded different levels of ERD (Doppelmayr et al., 1998a), which might also induce a dissociation of the poststimulus patterns of alpha dynamics. Additionally, a simulation was carried out for each of these subgroups to investigate whether all groups show evidence for phase-resetting.

4.2. Materials and Methods

Subjects and experimental procedure

Twenty-three subjects participated in this study (16 females, mean age 25; range 20-39 years). Subjects gave informed consent prior to the start of the experiment. This research was carried out in accordance with local ethics guidelines and the Declaration of Helsinki (World Medical Association: Ethical Principles for Medical Research Involving Human Subjects, 1964). All subjects had normal or corrected-to-normal vision and were free of neurological or psychiatric disorders. Recordings were made while subjects sat in a dimly lit, sound-attenuated and electrically shielded booth.

Black circles and squares on a white background were used as stimuli. Both types of stimuli appeared with equal probability. Stimuli were presented on a computer monitor placed at a distance of 105 cm in front of the subject. Monitor refresh rate was 100 Hz. Stimuli were displayed at a size of 8° visual angle and were presented centrally for a duration of 250 ms. Subjects were required to always remain centrally fixated. Stimulus presentation was followed by a variable inter-stimulus-interval ranging from

1000 to 1400 ms. Subjects were instructed to press a button with the thumb of one hand if the stimulus was a circle and to press a button with the other hand if the stimulus was a square. In order to analyze reaction times, subjects were asked to press the button as quickly as possible. Response hands were counterbalanced across subjects. The experiment consisted of 90 trials per type of stimulus (circle or square), resulting in a total number of 180 trials. For the purpose of the present analysis data were collapsed across both stimulus types. Two breaks of one minute duration were given in this experimental session.

Data acquisition

EEG was recorded using a high impedance 64 channel Net Amps 200 system (Electrical Geodesics, Eugene, Oregon) with Ag/AgCl-electrodes placed in an electrode cap (Easycap, Falk Minow Services, Munich) and a nose-tip reference. Sensor impedances were maintained below 20 kΩ prior to data acquisition (Ferree et al., 2001). EEG was analogue filtered from 0.1 to 100 Hz, digitized at 500 Hz and stored for off-line analysis. The present study is a reanalysis of the data published in Busch et al. (2004), which focuses on gamma activity.

Data were epoched from 500 ms before to 1000 ms after stimulus onset. Since the aim of the present study was to investigate the relation of prestimulus EEG activity and poststimulus EEG dynamics, no baseline correction was applied. Automatic artifact rejection excluded trials from averaging if the standard deviation within a moving 200 ms time interval exceeded 30 µV. Subsequently, all epochs were visually inspected for artifacts, and epochs containing eye-movements or electrode drifts were rejected. One subject had to be excluded from further analyses because of poor data quality.

Time-frequency analysis

For investigating the amplitude and time-course of oscillatory activity, the EEG signals were convolved with Morlet wavelets (Herrmann and Mecklinger, 2000; Herrmann et al., 2005). The wavelet transform was performed for each individual trial, and the absolute values of the resulting transforms were averaged. This measure of signal amplitude in single trials reflects the total activity for a certain frequency range, irrespective of whether it is phase-locked to the stimulus or not. We will refer to this measure as the total activity, since it comprises evoked as well as induced activity. On the other hand, to compute the evoked activity, which is, by definition, phase-locked to the stimulus, the wavelet transform was applied to the averaged evoked potential. In addition, the degree of phase-locking was calculated by means of the 'phase-locking factor', which reflects the homogeneity of the instantaneous phase across single trials. To this end, the phase of the complex wavelet decomposition in each single trial was represented as a point on the unit circle irrespective of amplitude. Averaging these points yields values between 0 for randomly distributed phases and 1 for phases that are strictly phase-locked to stimulus onset across trials.

Selection of the individual alpha frequency

It is well known that subjects differ considerably in their 'individual alpha frequency' (IAF; Doppelmayr et al., 1998b; Klimesch, 1999). Therefore, the frequencies used in the wavelet analyses of total and evoked alpha activity were determined individually for every subject. Time-frequency transforms were first computed for electrodes E58, E59 and E60 (equivalent to O1, OZ and O2 in the 10-10 system, respectively) and were subsequently averaged to increase the signal-to-noise ratio. From these averaged time-frequency scalograms individual alpha frequencies were obtained as the maximum of prestimulus total activity in the frequency range between 8 and 13 Hz in a time window from 300 to 200 ms prior to stimulus onset. If there was no detectable alpha peak, 10 Hz was selected as the individual alpha frequency for those subjects. This had to be done for eight subjects which were later assigned to the low-alpha group (see the following section).

Grouping subjects and statistical analysis

In order to inspect differences in the subsequent responses according to the amount of prestimulus total alpha activity, we categorized our subjects into three subgroups (high-, mid-, and low-alpha) according to their mean amplitude of prestimulus total alpha activity while trying to keep the size of the three groups as equal as possible. The seven subjects with highest amplitudes of prestimulus total alpha activity comprised the high-alpha group (mean amplitudes ranging from 6.2 µV to 9.9 µV). The next seven subjects with lower amplitudes comprised the mid-alpha group (mean amplitudes ranging from 3.9 µV to 5.6 µV) and the remaining eight subjects were assigned to the low-alpha group (mean amplitudes ranging from 2.0 µV to 3.2 µV).

For statistical analyses, total and evoked alpha activity were averaged across electrodes E58, E59 and E60 and analyzed within a time window from 0 to 400 ms after stimulus onset for the poststimulus onset responses. Since we did not apply a baseline correction in our analysis, we instead measured mean values of prestimulus total and evoked alpha activity and compared them statistically with the poststimulus individual amplitude. Baseline activity was measured as the mean of activity in the time window from 300 ms to 200 ms before stimulus onset. Baseline magnitudes were then compared with the maximum amplitude of evoked alpha activity in the time window from 0 to 400 ms poststimulus. For total alpha activity, we chose the same time window and compared baseline activity with minimum amplitudes of the high- and mid-alpha groups and maximum amplitudes for the low-alpha group, as the grand average of the high- and mid-alpha groups demonstrated a decrease, and that of the low-alpha group showed an increase after stimulation, as shown in Fig. 9A. The peak latencies of total and evoked alpha activity were also evaluated. All time windows were determined on the basis of the grand averages (cf. Fig. 9) and individual variances were taken into account.

Reaction times and accuracy (error rates) were also measured for behavioral analysis. In order to compare reaction times, error rates, mean amplitudes of prestimulus total alpha activity, mean frequencies of IAFs among three groups and peak latencies of total and evoked alpha activity, we performed a one-way ANOVA with a ‘group’ factor (high-alpha vs. mid-alpha vs. low-alpha group). In addition, the amplitudes of total and evoked activity were analyzed with a repeated measures ANOVA comprising the within-subjects factor ‘stimulation’ (baseline vs. onset response) and the between-subjects factor ‘group’ (high-alpha vs. mid-alpha vs. low-alpha group). In order to compare the peak latencies of poststimulus total alpha activity with those of poststimulus evoked alpha activity, we conducted a repeated measures ANOVA comprising the within-subjects factor ‘latency’ (peak latency of total activity vs. of evoked activity) and the between-subjects factor ‘group’ (high-alpha vs. mid-alpha vs. low-alpha group). Greenhouse-Geisser correction was used where appropriate. All subsequent post-hoc tests were Bonferroni-corrected for multiple comparisons, and only corrected *p*-values (the threefold of the original *p*-values) are reported.

Simulation of additive and non-additive signal generation processes

For our simulation analysis the same procedure as in the study by Hanslmayr et al. (2007) was used. The main idea of this simulation is that for the ‘additive power’ model the EEG signal, eeg(ij), for each sample point i and trial j can be described by two additive components. First, the background EEG amplitude b(ij) and second, the single trial evoked potential ep(ij) [1].

$$eeg(ij) = b(ij) + ep(ij) \quad [1]$$

For the 'phase-reset' model, the lack of an additive component leads to the prediction that the EEG signal remains equal to background EEG [2].

$$eeg(ij) = b(ij) \quad [2]$$

Note that in [2], b(ij) is assumed to undergo a phase-reset which is not the case for [1]. As mentioned above, testing for additivity would be easy and straightforward if there were no concurrent amplitude modulation of the background EEG. However, if the background EEG undergoes an amplitude change during the same time as evoked components are generated, the expected increase in amplitudes by evoked components may be masked by an event-related decrease in amplitudes. Therefore, we need to take into account this amplitude decrease in our simulation. As suggested by Hanslmayr et al. (2007) the amplitude of the background EEG can be estimated by subtracting the average ERP, i.e. ep(i), from each single trial. This measure is called 'non-phase-locked activity' (NP; or induced activity; see Kalcher and Pfurtscheller, 1995) and makes the assumption that the single-trial ep(ij) can be estimated by the average ep(i).

The simulation we used (Hanslmayr et al., 2007) comprised three steps:

1. We computed the time course of the 'non-phase-locked activity' (NP) for each individual's alpha activity. This was done by subtracting the average ERP from each single trial and computing the absolute values of all single trials which were then averaged.
2. Next, we generated artificial single trials (sine waves, randomly varying in phase) and multiplied these single trials with the individual NP computed in step 1.
3. Thereafter, we added the average ERP of an individual subject onto the single trials computed in step 2 and calculated the resulting envelope, which will be termed 'estimated activity'. The envelope was computed using the Hilbert transform implemented in 'Matlab software (The MathWorks Inc., USA; version 7.0)'. Finally, the 'estimated activity' was compared with the 'real activity' of the data (see below).

If the 'additive power' model were true, then amplitudes estimated by the simulation should equal the empirically observed amplitudes. If, however, these two values differ there must be non-linear processes involved. Hanslmayr et al. (2007) argued that in the latter case the 'phase-reset' model is more likely, since phase-resetting is a non-linear process.

The simulation was carried out separately for each subject. To estimate the alpha activity for the simulation, the unaveraged EEG data (collapsed across both stimulus types) were first bandpass filtered at the subjects' IAF. We employed a Butterworth filter without phase shift which is implemented in the 'Brain Vision Analyzer software (BrainProducts GmBH, Germany; version 1.05)' with a slope of 48 dB/octave and a bandwidth of 2 Hz. For the analysis of individual alpha frequencies we applied individual filter pass-bands around the subject's individual alpha frequency. Thus, for example, we took cutoff frequencies (-3 dB) at 9 Hz and 11 Hz for subjects with 10 Hz IAF.

For statistical analyses, the following procedures were carried out. At first, real activity and estimated activity were calculated for each subject. Next, t-tests were calculated for each sample point in the poststimulus interval for each group and electrode separately to determine whether the real activity is significantly different from the estimated activity in the simulation. To control for multiple testing, the *p*-level was set to 0.005 (two-tailed). Additionally, a two-way ANOVA was calculated with the factors 'group' (high-alpha vs. mid-alpha vs. low-alpha group) and 'activity' (real vs. estimated total activity averaged over all three channels from 0 to 500 ms poststimulus).

4.3. Results

The three groups differed significantly in the amplitude of prestimulus total alpha activity (F(2,19)= 69.315, *p*<.0005; high-alpha group: 7.9 μV; mid-alpha group: 4.7 μV; low-alpha group: 2.5 μV), while individual alpha frequencies did not differ significantly between groups (F(2,19)= .638, *ns*; high-alpha group: 10.4 Hz; mid-alpha group: 9.9 Hz; low-alpha group: 10.0 Hz). No significant differences between three groups were observed for reaction times (F(2,19)= .166, *ns*) or error rates (F(2,19)= 1.109, *ns*).

Total alpha activity changed in response to stimulation (F(1,19)= 37.638, *p*<.0005; cf. Figs. 9-12). A strong group effect indicated that the amplitudes of total alpha activity were significantly different between groups (F(2,19)= 44.790, *p*<.0005). Furthermore, the event-related change of total alpha activity relative to baseline differed between groups ('group' x 'stimulation': F(2,19)= 24.818, *p*<.0005). Post-hoc tests revealed that there was a significant decrease of total alpha activity in the high-alpha group (F(1,6)= 35.155, *p*<.005; baseline: 7.9 μV; onset: 4.1 μV) and in the mid-alpha group (F(1,6)= 10.638, *p*=.051; baseline: 4.7 μV; onset: 3.2 μV) but a significant increase of total alpha activity in the low-alpha group (F(1,7)= 11.326, *p*<.05; baseline: 2.5 μV; onset: 3.0 μV; cf. Figs. 9A and 10A). As for the peak latencies of poststimulus total alpha activity, the three groups differed significantly (F(2,19)= 61.868, *p*<.0005). Post-hoc tests indicated that the latencies in the low-alpha group (mean: 106.9 ms) were significantly earlier than those in the high-alpha group (F(1,13)= 103.780, *p*<.005; mean: 291.0 ms) and in the mid-alpha group (F(1,13)= 111.056, *p*<.005; mean: 328.2 ms).

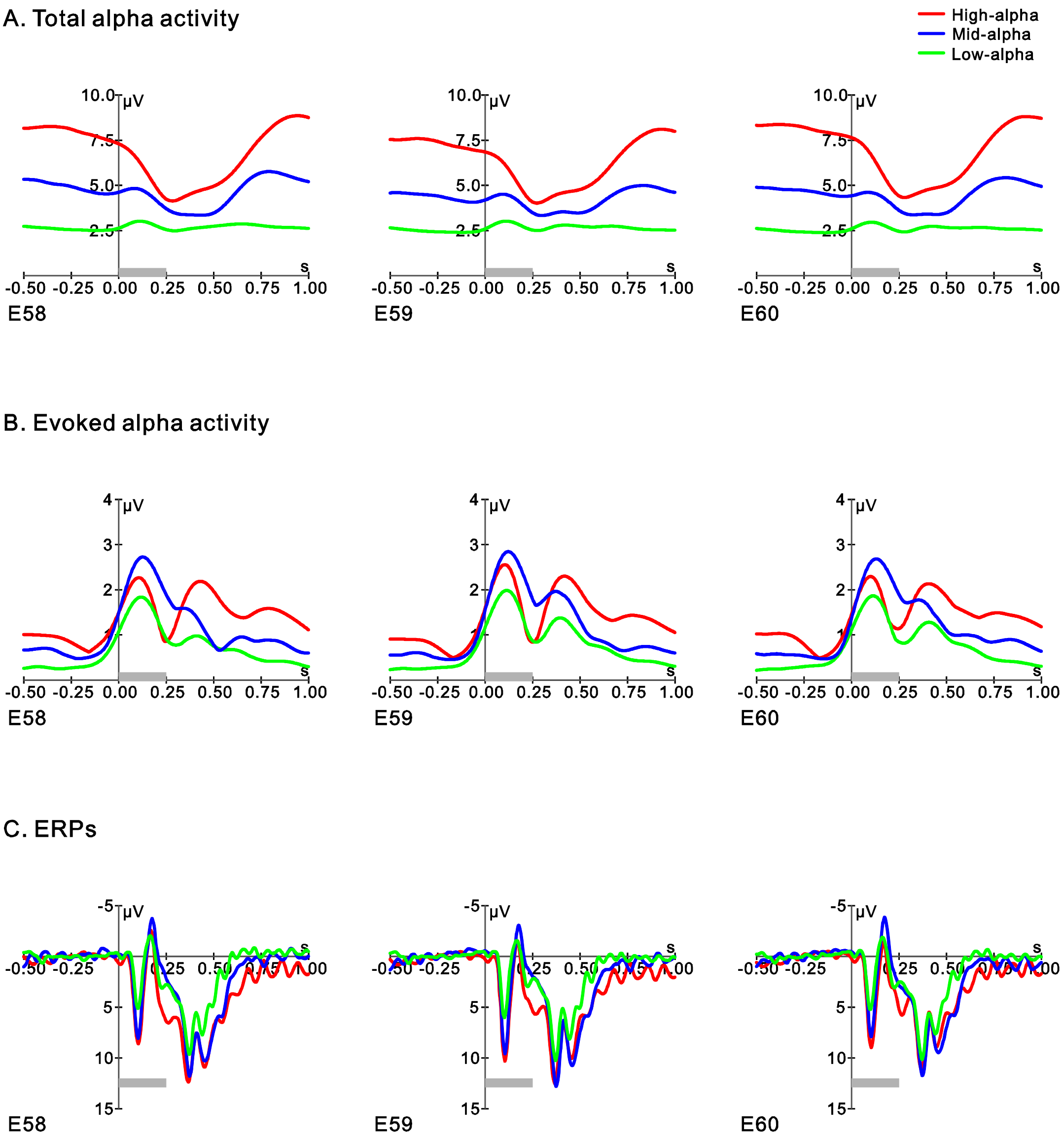


Figure 9. Grand averaged time courses of (A) total, (B) evoked alpha activity and (C) ERPs at the occipital electrodes (E58, E59 and E60) for all three groups (red lines: high-alpha group; blue lines: mid-alpha group; green lines: low-alpha group). For displaying ERPs, we performed 20 Hz low-pass filtering and a baseline correction by subtracting mean amplitudes from 300 to 200 ms prestimulus. Gray bars indicate stimulus duration.

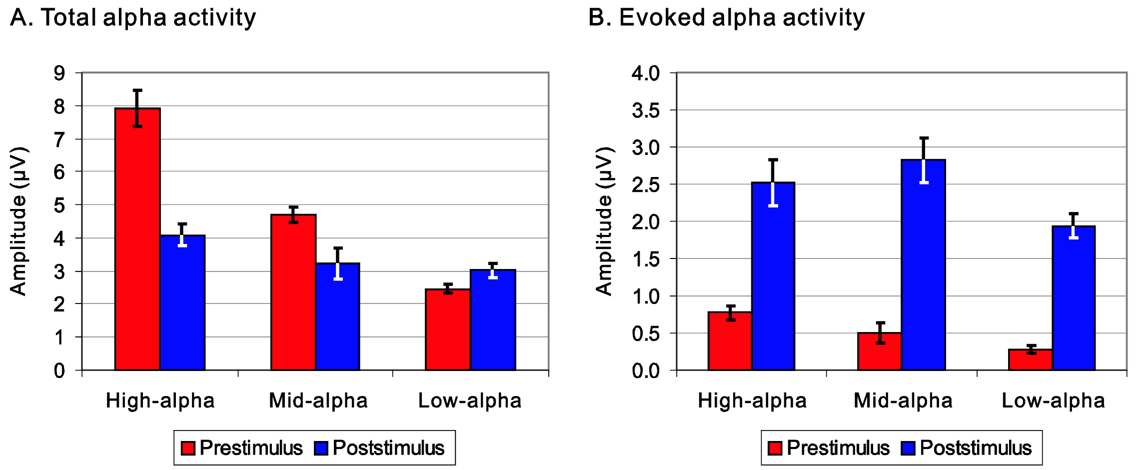


Figure 10. Categorized bar graphs with error bars for (A) total and (B) evoked alpha activity of both prestimulus and poststimulus activity averaged across electrodes E58, E59 and E60 for all groups. Red columns indicate prestimulus activity and blue columns poststimulus activity. Error bars represent ±1 standard error of the mean. All subjects demonstrate an increase of evoked alpha activity in response to stimulation. However, only the high- and mid-alpha groups show a decrease of total alpha activity which is considered alpha-blocking. In the low-alpha group a significant increase of total alpha activity is visible instead of alpha-blocking.

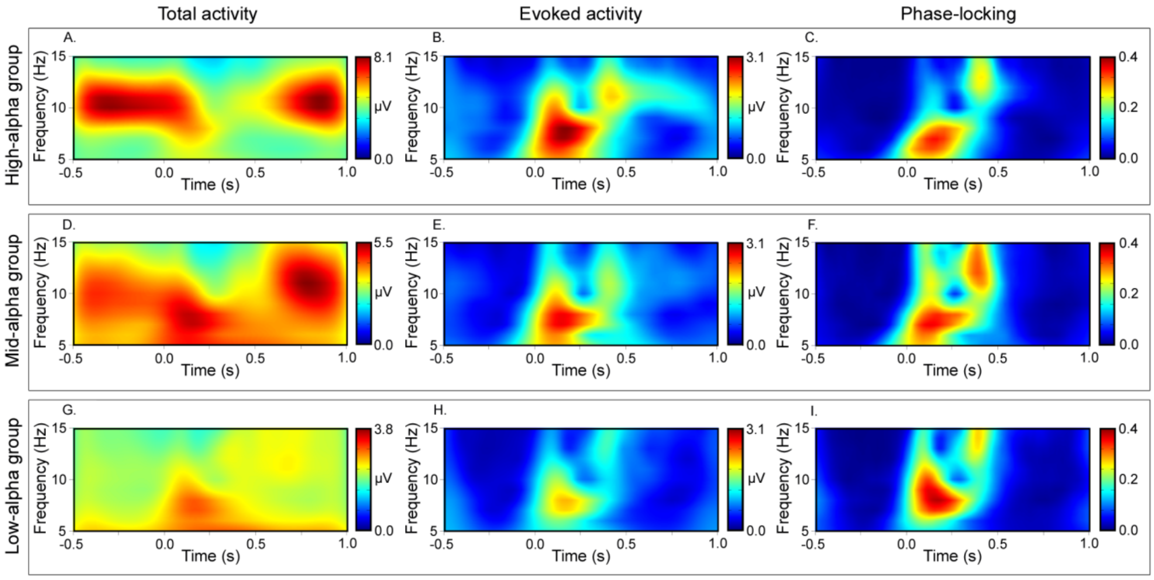
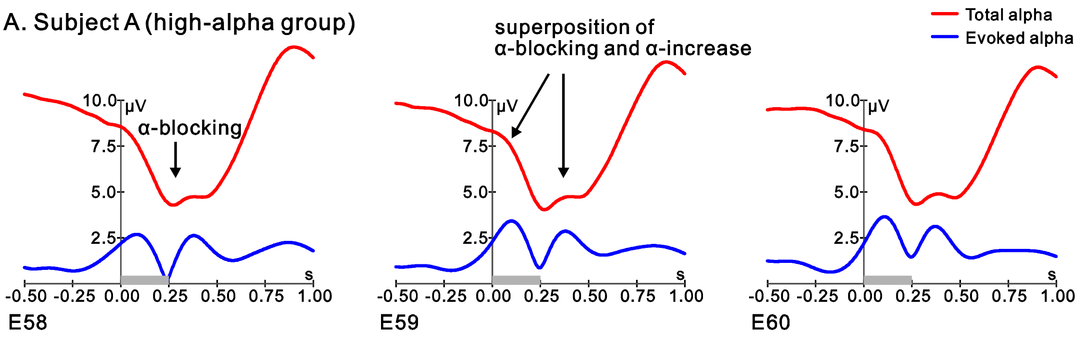
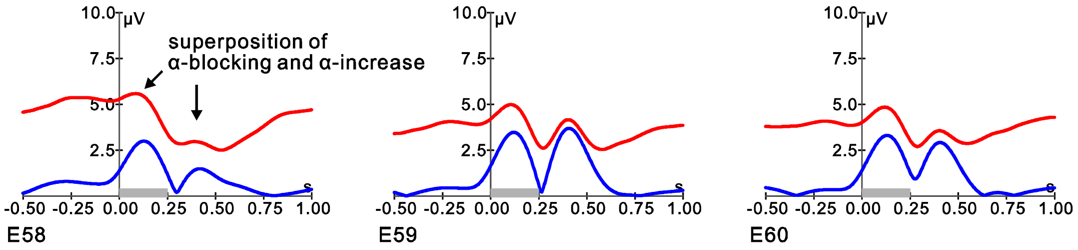


Figure 11. Time-frequency representations of total activity (A, D and G); evoked activity (B, E and H); phase-locking factor (C, F and I) averaged across electrodes E58, E59 and E60 for all groups. All plots are grand-averaged. High- and mid-alpha groups show prominent prestimulus alpha activity which is almost absent in the low-alpha group (cf. between -500 and 0 ms in A, D and G). Stimuli were presented from 0 to 250 ms.

A. Subject A (high-alpha group)



B. Subject B (mid-alpha group)



C. Subject C (low-alpha group)

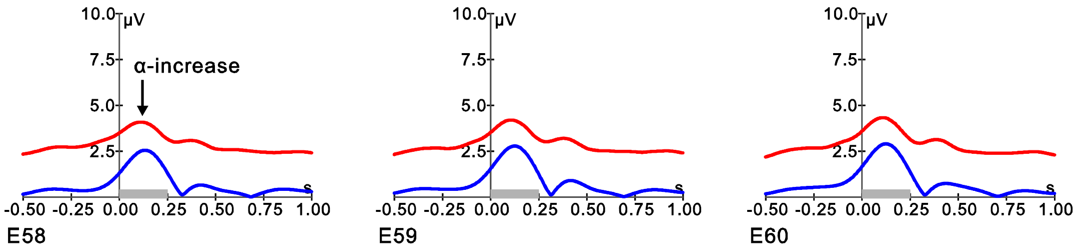


Figure 12. Total and evoked alpha activity at the occipital electrodes (E58, E59 and E60) of one representative single subject for each group (red lines: total alpha activity; blue lines: evoked alpha activity). Gray bars indicate stimulus duration. Subject A of the high-alpha group shows a prominent decrease of total alpha activity while subject C of the low-alpha group reveals an increase of total alpha activity after stimulation. In subject A and B, a superposition of such an increase and a decrease in the poststimulus total alpha activity can be seen.

On the other hand, evoked alpha activity increased in response to stimulation (F(1,19)= 157.262, *p*<.0005; cf. Figs. 9-12). Moreover, the three groups differed in the amplitude of evoked alpha activity (F(2,19)= 4.809, *p*<.05), but there was no significant interaction ('group' x 'stimulation': F(2,19)= 1.836, *ns*). The peak latencies of evoked alpha activity were not significantly different between groups (F(2,19)= 1.142, *ns*; high-alpha group: 107.7 ms; mid-alpha group: 129.7 ms; low-alpha group: 118.0 ms).

Furthermore, the peak latencies of evoked alpha activity were significantly different from those of total alpha activity (F(1,19)=183.991, *p*<.0005), and there was a significant interaction ('group' x 'latency': F(2,19)= 57.364, *p*<.0005). Post-hoc tests revealed a significant main effect for the factor 'latency' in the high-alpha group (F(1,6)=222.244, *p*<.0005) and the mid-alpha group (F(1,6)=66.762, *p*<.0005), whereas the low-alpha group showed no significant differences (F(1,7)=2.037, *ns*).

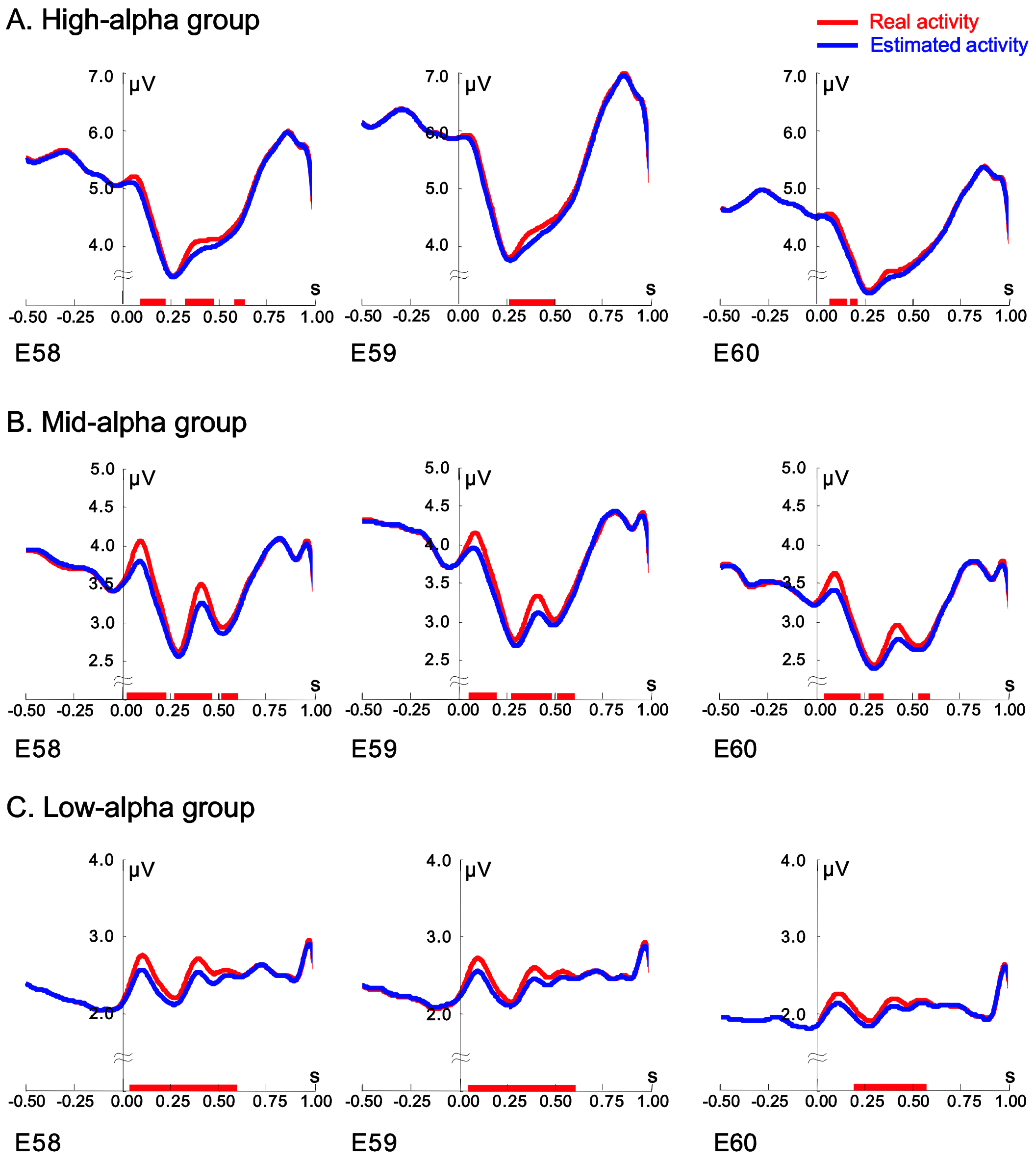


Figure 13. Results of the simulation of total signal activity for the (A) high-alpha, (B) mid-alpha and (C) low-alpha group are plotted. Red lines correspond to the real activity and blue lines correspond to the signal activity estimated by the simulation. Red bars indicate the time interval at which the real and the estimated activity differ significantly from each other (*p*<.005; two-tailed). Note that the real activity is different from the estimated activity in the simulation in all three groups.

The results of the simulation revealed that the real activity was significantly different from the estimated activity in the simulation for each group and channel (see Fig. 13). The ANOVA showed a significant main effect for the factor 'activity' (F(1,19)=20.266, *p*<.001) indicating that the activity estimated by the simulation was smaller than the real activity. A significant main effect for the factor 'group' (F(2,19)=28.468, *p*<.001) and a significant 'group' x 'activity' interaction (F(2,19)=10.274, *p*<.001) showed a stronger difference between real and estimated activity for the low alpha group compared with the two others.

4.4. Discussion

In this study, we investigated the relationship between event-related oscillatory activity in the alpha band and prestimulus levels of ongoing alpha activity. Our results demonstrate that the amount of prestimulus alpha activity modulates the subsequent event-related neural response. Similar findings about ERD/ERS in the alpha band (Pfurtscheller, 1992; Pfurtscheller et al., 1996; Pfurtscheller, 2001) and a power-increase in intracortical recordings (Fell et al., 2004; Shah et al., 2004) have been reported before. Here we observed different event-related alpha dynamics in terms of total and evoked activity in a single framework with respect to ERP-generation to evaluate a plausible model for ERP-generation.

As Doppelmayr et al. (1998a) found that the prestimulus level of absolute band power has a strong influence on ERD, in the high- and mid-alpha groups we observed a typical poststimulus alpha-blocking which seemed to be absent in the low-alpha group (cf. Figs. 9A, 10A, 11A, 11D, 11G and 12). One possible explanation for this difference is that those subjects in the high- and mid-alpha groups are more susceptible to desynchronization of their synchronized prestimulus alpha activity than those with low levels of prestimulus alpha activity (low-alpha group).

In the high- and mid-alpha groups, we observed significantly later peaks of total than of evoked alpha activity. These findings suggest that there are different underlying mechanisms for phase-locked and non-phase-locked alpha activity.

Evidence for phase-resetting

The evoked alpha activity of all groups exhibited an obvious increase after stimulation (cf. Fig. 9B). Thus, we found a dissociation between a decrease of total alpha activity and an increase of evoked alpha activity in the high- and mid-alpha groups, as shown in Figs. 9A and 9B. Since phase-resetting can occur independently of the modulation of total activity, these observations from subjects with higher prestimulus alpha activity can be better explained by poststimulus phase-resetting of the ongoing alpha activity. However, we are reluctant to interpret this poststimulus dissociation between an increase of evoked alpha and a decrease of total alpha activity as evidence for pure phase-resetting, because single subject data in the high- and mid-alpha groups (cf. Figs. 12A and 12B) demonstrated a tiny increment of the poststimulus total alpha activity superimposed on its decrease when evoked alpha increased. In these cases, a majority of poststimulus total alpha enhancement seemed to be masked by prominent alpha-blocking, as suggested in the introduction section. Thus, we complementarily referred to our simulation results, which substantiated that there was evidence for a non-linear contribution for ERP-generation in all three groups. Accordingly, we assume that phase-resetting contributed here because phase-resetting is a non-linear process whereas additive power is a linear process.

Such an evidence of phase-resetting is in line with the observations and conclusions reached by other previous studies (Brandt, 1997; Gruber et al., 2005; Hanslmayr et al., 2007). For example, Brandt (1997) reported that the first two poststimulus negative peaks of the ERP undergo phase and prestimulus amplitude sensitive latency reorganization during presentation of both visual and auditory paradigms. These findings consistently suggest that stimulation induces a rearrangement of ongoing EEG activity reflected in the attributes of subsequent responses.

A recent report of a failure to find phase-resetting in posterior alpha activity seems to be contradictory to our findings (Mazaheri and Jensen, 2006). Using a measure termed the phase-preservation index the authors reported that in single trials the alpha oscillations after visual stimuli preserved their phase relationship with respect to the phase before the stimuli. However, this study did not show considerable poststimulus phase-locking within the alpha band. This may be due to the attributes of their stimuli: wedge-shaped checkerboards displayed at a width of 12° visual angle. Only a small portion of the stimuli was projected to the macula, and the largest part of the wedge-shaped checkerboards was presented peripherally. These factors of stimulus size and eccentricity may have led to their failure to observe significant phase-locking. If, however, not even significant phase-locking could be observed – which is typically present both in phase-resetting and in additive power, the authors were not likely to find evidence for phase-resetting.

Evidence for additive power

In addition, we observed that the total alpha activity of the low-alpha group showed an increase while evoked alpha activity simultaneously increased in response to stimulation (cf. Figs. 9A, 9B, 10A, 10B, 11G and 11H). Even single subject data (cf. Fig. 12C) revealed a simultaneous increase of poststimulus total *and* evoked alpha activity. Although these findings do not directly imply the validity of an additive component, they seem to be more in accordance with the additive power model since in the additive power model phase synchronization can occur only together with an increase in total power when the evoked component appears.

Beside these observations, results from our simulation suggest that phase-resetting alone could not account for ERP-generation because the estimated activity was not always significantly different from the real activity in the simulation. Our time-frequency scalograms of phase-locking also display that all three groups exhibit an increase in phase-locking factors irrespective of the amount of prestimulus total alpha activity (cf. Fig. 11). This may imply a poststimulus additive power independent of prestimulus conditions. Moreover, recent reports based on depth recordings consistently demonstrated an obvious increase in EEG power accompanied by phase concentration at the dominant frequency of the ERP (Fell et al., 2004; Shah et al., 2004).

Coexistence of both models

Taken together, all of these phenomena imply that the 'phase-reset' and the 'additive power' models are evenly plausible within a single framework and able to coexist. We recently demonstrated that phase-locking and amplitude modulations of alpha activity reflect different cognitive mechanisms (Herrmann et al., 2004c). Thus, it seems plausible to assume both modulations to occur, however at different degrees depending on cognitive performance as well as prestimulus activity. An auditory study by Fuentemilla et al. (2006) consistently provided that both models are plausible, depending on the stimulation condition. They found that the 'additive power' model was most likely to explain responses to the first presented stimulus but phase-resetting was a more plausible mechanism when stimuli were presented as second or third in a row. A common interpretation of their and our observations is that the dynamics of the alpha band response depends upon the prestimulus brain condition.

More generally, these studies fully support a dynamic view of brain function. The recently proposed event-related brain dynamics model (ERBD; Makeig et al., 2004) provides a valuable framework for future research in this field. In this model, phase-consistency, additive power and frequency span a 3-dimensional signal space. Within this 3-D space, the ERBD illustrates the relationship between additive ERPs, partial phase resetting and ERS/ERD. The ERBD model also provides a valuable context for the multimodal integration of EEG and fMRI (Debener et al., 2005; Debener et al., 2006). It is likely that only additive brain responses, that is, some areas of the ERBD signal space, systematically correlate with the fMRI BOLD signal, whereas ERPs related to partial phase-resetting may not correlate with the BOLD signal (Fell et al., 2004; Debener et al., 2006). A detailed analysis of individual differences in EEG alpha activity in this context, as demonstrated in the present study, may provide further insights.

Functions of prestimulus alpha activity

In line with our findings, effects of prestimulus alpha activity on subsequent brain responses have been documented in previous reports (Brandt et al., 1991; Brandt and Jansen, 1991; Rahn and Basar, 1993b; Price, 1997; Doppelmayr et al., 1998a; Fingelkurts et al., 2002). Walter and Walter (1949) reported that different patterns of alpha activity after eye-closing were observed according to the features of spontaneous (or resting) alpha activity. Similarly, we observed that there was even poststimulus enhancement in total alpha activity in the low-alpha group, which seems to be in conflict with the phenomenon of alpha-blocking after stimulation. This corroborates the notion that the level of alpha-blocking depends on the substantial existence of prestimulus alpha activity as Doppelmayr et al. (1998a) reported.

For many years, the background EEG alpha activity had been regarded as representing mere 'idling' of the brain (Adrian and Matthews, 1934; Pfurtscheller et al., 1996). However, it has recently been considered as serving a certain active control with respect to mental processes (Petsche et al., 1986; Basar et al., 1997; Cooper et al., 2003). In addition, it has been proposed that integrative cognitive functions are carried out by large-scale neural networks (Bressler, 1995) and that this global binding of local networks may be accomplished by alpha activity (Nunez et al., 2001; Sauseng et al., 2005a). Indeed, a growing body of evidence suggests that prestimulus EEG alpha activity may be involved in higher cognitive functions such as memory performance (Klimesch, 1999), anticipation (Klimesch et al., 1998; Maltseva et al., 2000) and sensory awareness (Varela et al., 1981; Palva et al., 2005). For example, Palva et al. (2005) demonstrated that the phase of ongoing cortical activity biases subsequent perception and that the widespread alpha-band component appears dominant for consciously perceived stimuli. Consistently, non-stimulus-locked alpha-band neural synchrony in the cat cortex was prominent in responses to expected objects but not in those to novel objects, which clearly indicated a role for alpha-band synchrony in top-down modulation (von Stein et al., 2000). Therefore, ongoing alpha activity before stimulation may play a functional role reflecting an aspect of the brain's readiness state relevant to an upcoming stimulus.

Consequently, different levels of prestimulus alpha activity induce different cognitive performance. Indeed, it has recently been reported that low prestimulus alpha leads to a good performance in a perception task (Ergenoglu et al., 2004; Hanslmayr et al., 2005) and a poor performance in a memory task (Hanslmayr et al., 2005). According to our results, this different cognitive performance should also be reflected in different poststimulus alpha dynamics. However, their functional relationship remains an open question and requires further investigation in future research.

Conclusion

In sum, at least in the alpha frequency domain, it is plausible that both 'phase-resetting' and 'additive power' could occur together after stimulation. Our observations of poststimulus dissociation between an increase in evoked alpha and a decrease in total alpha seem to be in favor of phase-resetting of ongoing EEG alpha activity, but a minor increase of total activity was detected when evoked activity enhanced even during such a dissociable poststimulus dynamics. Thus, we referred to the simulation results and confirmed that a non-linear contribution occurred after stimulation, which provides us with evidence for phase-resetting. On the other hand, a concurrent enhancement of poststimulus evoked and total alpha activity seems in line with the 'additive power' model. In agreement with the ERBD model (Makeig et al., 2004), both partial phase-resetting and partial additive power contribute dynamically to generate ERPs.

Chapter 5: Prestimulus alpha activity and ERP dynamics (Study 2)

The experimental results presented in this chapter are currently under review at the journal *Clinical Neurophysiology*.

5.1. Introduction

To date, it remains an open question whether event-related potential (ERP) components result from phase-resetting of ongoing EEG activity (Sayers et al., 1974; Basar, 1980b; Brandt, 1992; Makeig et al., 2002; Makeig et al., 2004; Mazaheri and Picton, 2005; Jansen et al., 2006) or from a stimulus-induced increase in EEG power (Jervis et al., 1983; Schroeder et al., 1995; Pfurtscheller and Lopes da Silva, 1999). In the 'phase-reset' model, sensory stimulation drives ongoing random-phase oscillations to act together in a coupled and coherent manner. In contrast, traditional conceptions of the ERP (the 'additive power' model) assume that an additional neuronal response in each trial, is additive to and independent of ongoing brain activity. In Study 1 (Chapter 4; Min et al., 2007), our simulation results indicated that non-linear processes contribute to ERP-generation. Here, we investigated whether these poststimulus non-linear processes are due to phase-resetting of prestimulus alpha activity.

Several studies exist on phase-resetting in relation to the generation of ERPs (Sayers et al., 1974; Makeig et al., 2002; Klimesch et al., 2004a; Klimesch et al., 2004b; Gruber et al., 2005). However, most of these studies focused on *poststimulus* EEG, in which one cannot easily verify the existence of phase-resetting simply on the basis of ERPs or phase-concentration (Jervis et al., 1983; Yeung et al., 2004; Gruber et al., 2005; Lakatos et al., 2005). ERP waveforms are computed by signal averaging across multiple EEG trials or epochs, time-locked to a certain class of events, and thus an increase in phase-locking *per se* is not informative about the generating mechanism because either phase reorganization or additive responses with fixed latency and polarity in each trial can produce an increase of inter-trial phase consistency.

It is worth considering several ways of investigating phase-resetting. For example, if there is a relative change in the direction of a *poststimulus* ERP modulation according to a certain attribute of *prestimulus* ongoing activity, this could be taken as evidence for phase-reorganization of ongoing activity. Indeed, there are some studies on the relationship between the amount of *prestimulus* alpha power and the *poststimulus* ERP components (Basar, 1980b; Basar and Stampfer, 1985; Brandt et al., 1991; Brandt and Jansen, 1991; Jansen and Brandt, 1991; Rahn and Basar, 1993a, b; Brandt, 1997; Barry et al., 2000). However, the exact relationship between prestimulus and poststimulus EEG activity remains controversial. Brandt's and Barry's groups have reported that greater prestimulus alpha amplitude led to larger ERP amplitudes – for example, the peak-to-peak amplitude of the N1 and P2 components (Brandt et al., 1991; Brandt and Jansen, 1991; Jansen and Brandt, 1991; Brandt, 1997; Barry et al., 2000), whereas Basar's group has found an inverse relation between prestimulus root-mean-square (RMS) alpha power and subsequent ERP amplitudes (Basar, 1980b; Basar and Stampfer, 1985; Rahn and Basar, 1993a, b). The attribute 'amount' of ongoing activity may alone not be specific enough to identify features of ongoing activity responsible for phase-resetting.

Rather, in order to test phase-resetting of ongoing activity, the attribute 'dominance' seems to be a more appropriate parameter than the 'amount'[17]. Phase-concentration has been predicted to take place in a certain frequency range that is evident as *dominant* ongoing oscillations already during a *prestimulus* interval (Makeig et al., 2002; Makeig et al., 2004; Gruber et al., 2005). For example, if a slow wave of high amplitude undergoes a transition, the power may disperse and shift to faster rhythms of lower power (Maloney et al., 1997). That is, if the dominant ongoing activity is absent, the necessary amount of prestimulus activity for upcoming phase-resetting may be missing, resulting in a failure to effectively reorganize and influence poststimulus activity.

Fortunately, it is a common observation that spontaneous alpha activity (prominent at occipito-parietal scalp sites during relaxed wakefulness) is dominant compared to other frequency bands (Adrian and Matthews, 1934; Niedermeyer, 1999). Indeed, delta activity (below 4 Hz) tends to be of the highest amplitude according to a '1/*f*-like' distribution in power-spectral densities[18], but only the alpha band typically

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[17] Although the concepts 'amount' and 'dominance' of activity may be highly correlated, the attributes themselves are distinct. For instance, the 'amount' of a certain activity is measured irrespective of activity in other frequency bands, whereas 'dominance' is defined in relation to the power of other frequencies. Therefore, individuals with high absolute alpha activity are not necessarily characterized by 'dominant' activity in the alpha band.

[18] The '1/*f*-like' power spectral distribution is a ubiquitous characteristic of complex systems, in which the power spectrum of a given time series is dominated by an inverse power law, resulting in an inverse linear relation between log frequency and log power, and such a '1/*f*-like' power

violates and significantly exceeds its limits roughly delineated by such a '1/*f*-like' distribution (cf. Fig. 14). Therefore, here we investigate whether prestimulus dominance of ongoing alpha activity influences poststimulus ERPs. Such an influence would constitute a violation of traditional assumptions of ERP-generation.

5.2. Materials and Methods

Subjects and experimental procedure

Twenty-three subjects were involved in this study (16 females, mean age 25; range 20-39 years) and gave their written informed consent. Our study was in accordance with local ethics guidelines and the Declaration of Helsinki (World Medical Association: Ethical Principles for Medical Research Involving Human Subjects, 1964). Subjects reported no history of neurological or psychiatric disorders and had normal or corrected-to-normal vision.

Black circles and squares on a white background were used as stimuli. Stimuli were presented on a computer monitor placed at a distance of 105 cm in front of the subject. The monitor refresh rate was 100 Hz. Stimuli were displayed at a size of 8° visual angle and were presented centrally for a duration of 250 ms. Stimulus presentation was followed by a variable inter-stimulus-interval ranging from 1000 to 1400 ms.

Subjects were instructed to always maintain central fixation and to press a button with the thumb of one hand if the stimulus was a circle. Upon presentation of a square, they were instructed to respond with the other hand. In order to analyze reaction times, subjects were asked to press the button as quickly as possible. Response hands were counterbalanced across subjects. Both types of stimuli appeared with equal probability, so that there were 90 trials per type of stimulus (circle or square), resulting in a total number of 180 trials. Two breaks of one minute duration were given in this experimental session. For the purpose of the present analysis, data were collapsed across both stimulus types.

EEG was recorded using a high impedance 64 channel Net Amps 200 system (Electrical Geodesics, Eugene, Oregon) with Ag/AgCl-electrodes placed in an electrode

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spectrum scaling has been studied in relation to power-spectral densities of EEGs (Pritchard, 1992; Chen et al., 1998; Freeman et al., 2003; Freeman, 2006).

cap (Easycap, Falk Minow Services, Munich) and a nose-tip reference. Sensor impedances were kept below 20 kΩ prior to data acquisition (Ferree, 2006). EEG was analogue filtered from 0.1 to 100 Hz, digitized at 500 Hz and stored for off-line analysis. Recordings were made while subjects sat in a dimly lit, sound-reduced and electrically shielded booth. This report represents a new analysis of a previously published dataset (Busch et al., 2004; Min et al., 2007).

Data analyses

Data were epoched from 500 ms before to 1000 ms after stimulus onset. Automatic artifact rejection excluded trials from averaging if the standard deviation within a moving 200 ms time interval exceeded 30 µV. Subsequently, all epochs were visually inspected for artifacts, and epochs containing eye-movements or electrode drifts were rejected. One subject had to be excluded from further analyses because of poor data quality.

For computing the wavelet transformation, the EEG signals were convolved with Morlet wavelets (Herrmann and Mecklinger, 2000; Demiralp and Ademoglu, 2001; Herrmann et al., 2005). To measure the prestimulus alpha amplitude, we computed total activity. For obtaining total activity, the wavelet transform was performed for each individual trial, and the absolute values of the resulting transforms were averaged. This measure thus reflects the total activity for a certain frequency range. Since the aim of the present study was to investigate the contribution of prestimulus alpha activity to subsequent ERPs, no baseline correction was applied to the wavelet transformation.

It is known that individuals differ in their 'individual alpha frequency' (IAF; Doppelmayr et al., 1998b; Klimesch, 1999; Gruber et al., 2005). Therefore, the alpha frequencies used in the present analyses were determined individually for every subject. Time-frequency transforms were first computed for three selected centro-parietal electrodes E52, E55 and E56 (approximately equivalent to Pz, PO3 and PO4 in 10-10 system, respectively)[19] and were subsequently averaged across these electrodes. From these averaged time-frequency scalograms 'individual alpha frequencies' were obtained as the maximum response of 'total activity' in the frequency range between 8 and 13 Hz in a time window from 300 to 200 ms prior to stimulus onset. If there was no prominent

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[19] This region was chosen because the amplitudes of prestimulus total alpha activity were most pronounced there (refer to the marked electrodes in Fig. 16).

alpha activity (i.e. no local maximum within such a time-frequency range), we took 10 Hz as the individual alpha frequency for those subjects. This was necessary for two participants, who were later classified into the non-dominant alpha group (see below).

In order to evaluate the impact of the dominance of prestimulus alpha activity, we assigned all subjects into one of two subgroups (dominant and non-dominant alpha groups) according to whether their prestimulus (from 300 to 200 ms prestimulus) mean amplitude of alpha band (IAF±2 Hz), averaged across the above three selected centro-parietal electrodes, was greater than the prestimulus mean amplitudes of the other three frequency bands: theta (from 4 to IAF-2 Hz), beta (from IAF+2 to 30 Hz) and gamma (from 30 to 50 Hz).[20] Such subjects were classified in the 'dominant alpha group'; otherwise, subjects were categorized into the 'non-dominant alpha group'. As a result, 13 subjects were assigned to the dominant alpha group and the remaining 9 subjects were categorized into the non-dominant alpha group.

A baseline correction for the ERP calculation was performed by subtracting the mean amplitudes in a baseline time window from 300 to 200 ms prestimulus. All ERP time windows (P1: 70 to 140 ms poststimulus; N1: 130 to 200 ms poststimulus) were determined on the basis of the grand averages and individual variances were taken into account. We evaluated the amplitudes and latencies averaged across three occipital electrodes E58, E59 and E60 (equivalent to O1, Oz and O2 in 10-10 system, respectively) for the P1 analysis, whereas we assessed the amplitudes and latencies averaged across two occipito-parietal electrodes E41 and E49 (equivalent to PO7 and PO8 in 10-10 system, respectively) for the N1 analysis. Such individual regions were selected where the ERP-amplitudes were most pronounced (see the areas with marked electrodes in Fig. 16), consistent with previous topographic studies of those ERP components (Di Russo et al., 2002; Horovitz et al., 2004). Reaction times and accuracy (error rates) were also measured for behavioral analysis. For statistical analysis, we employed a one-way ANOVA with a factor 'group' (dominant vs. non-dominant alpha group). Additionally, to examine a correlation between the 'dominance' and the 'amplitude' of prestimulus total alpha activity, we computed Pearson correlations (two-tailed).

5.3. Results

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[20] We excluded the delta band (below 4 Hz) from the present analysis not only because of its intrinsic tendency of the highest amplitude according to '1/*f*-like' distribution in power-spectral densities, but also because of possible artifacts due to slow potential drifts.

The mean values of the individual alpha frequencies were not significantly different between groups (F(1,20)= .114, *ns*; dominant alpha group: 10.6 Hz; non-dominant alpha group: 10.8 Hz). However, as expected, the amplitudes of prestimulus total alpha activity in the dominant alpha group were significantly higher than in the non-dominant alpha group (F(1,20)= 11.907, *p*<.005; dominant alpha group: 7.6 µV; non-dominant alpha group: 3.3 µV; cf. Fig. 14). Pearson correlations between 'dominance' and 'amplitude' of prestimulus alpha activity revealed a strong correlation (r(22)= .611, *p*<.005).

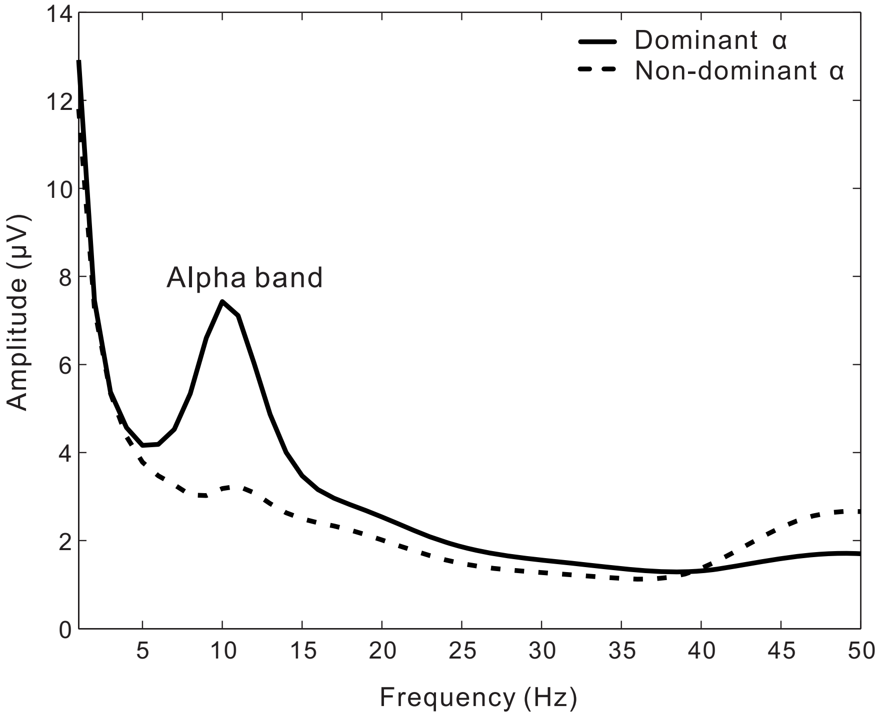


Figure 14. Amplitude spectrum of prestimulus EEG epochs (from 300 to 200 ms prestimulus) averaged across the three centro-parietal electrodes (E52, E55 and E56) from both groups (solid line: dominant alpha group, dashed line: non-dominant alpha group). Notice the difference of amplitudes between both groups around the alpha band.

Behavioral data

There was no significant difference in reaction times between the two groups (F(1,20)= .347, *ns*). In addition, no effects approached statistical significance in the accuracy of task-performance (F(1,20)= 1.459, *ns*).

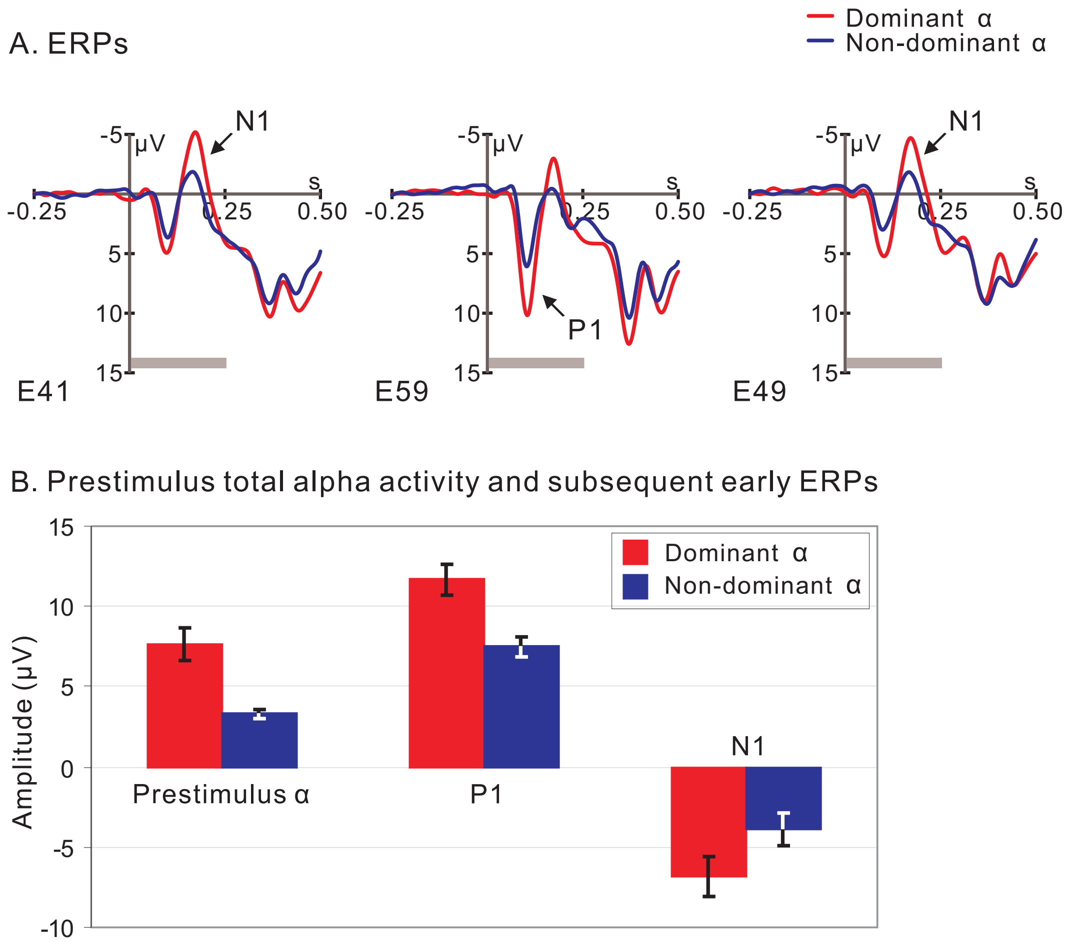


Figure 15. (A) Grand-averaged ERPs at three representative posterior electrodes for both groups (red lines: dominant alpha group, blue lines: non-dominant alpha group). Notice P1 and N1 amplitudes around 100 ms and 170 ms poststimulus, respectively. For the display of ERPs, we performed 20 Hz low-pass filtering and a baseline correction. Gray bars indicate stimulus duration. (B) bar graphs with error bars for the prestimulus total alpha activity, P1 and N1 amplitudes averaged across the corresponding electrodes (see text) representing their maximal amplitudes for both groups (red columns: dominant alpha group, blue columns: non-dominant alpha group). Error bars represent ±1 standard error of the mean.

ERP components P1 and N1

As shown in Figs. 15 and 16, the P1 amplitudes were significantly larger in the dominant alpha group than in the non-dominant alpha group (F(1,20)= 10.854, $p<.005$; dominant alpha group: 11.7 μV, non-dominant alpha group: 7.5 μV), while their peak latencies were not significantly different (F(1,20)= 1.159, *ns*). On the other hand, the ANOVA revealed no significant difference for the N1 amplitudes between these groups (F(1,20)= 2.888, *ns*) or their peak latencies (F(1,20)= 1.423, *ns*). The topographical distributions for P1, N1 and prestimulus total alpha activity are presented in Fig. 16. Prestimulus total alpha activity was evident at centro-parietal scalp sites, and P1 amplitudes were largest at occipital electrodes. The N1 topography showed a more bilateral, occipital distribution (see the marked electrodes representing each activation area in Fig. 16).

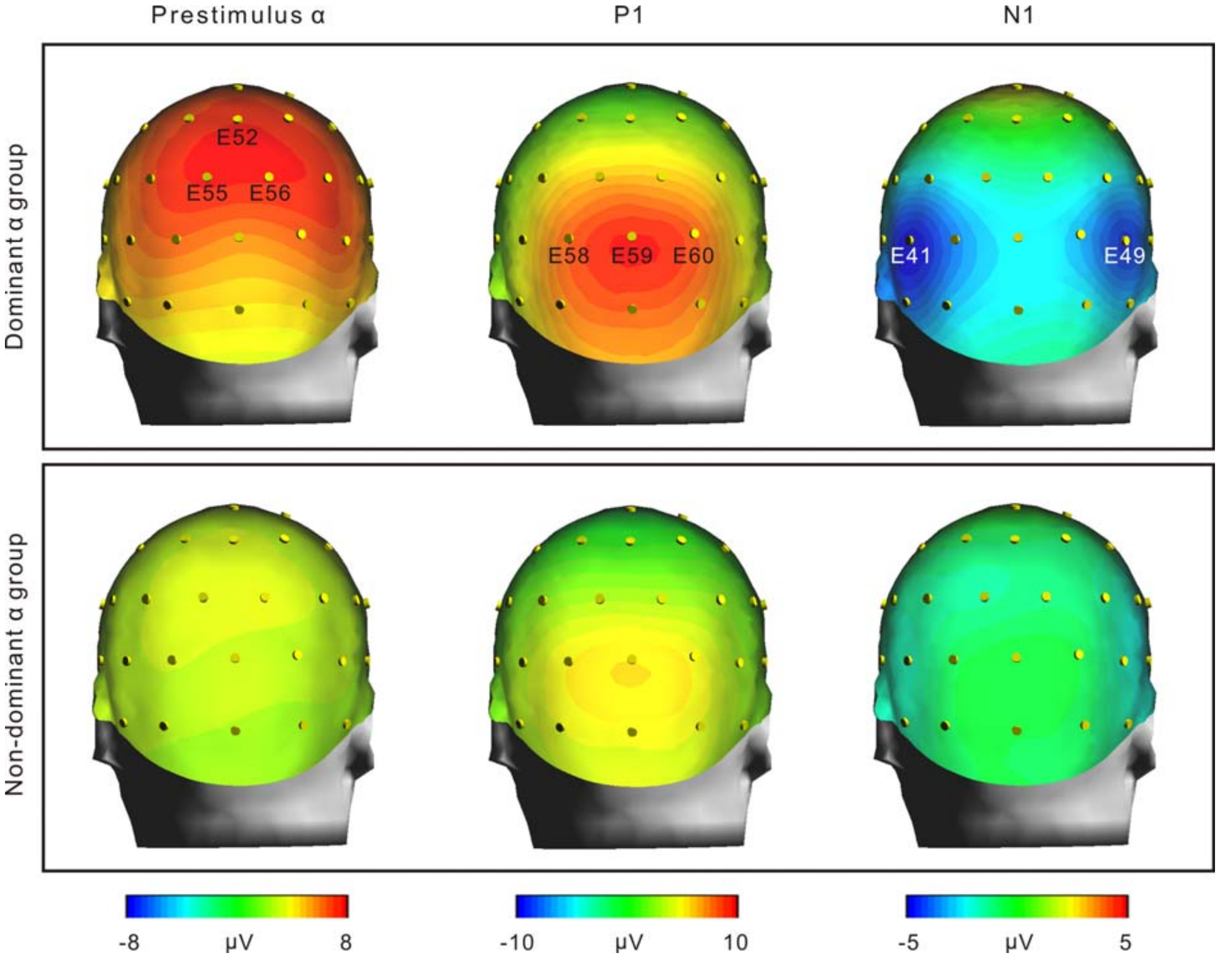


Figure 16. Topographies of prestimulus total alpha activity, P1 and N1 in both groups (upper row: dominant alpha group, lower row: non-dominant alpha group). Note that the topography of prestimulus alpha activity overlaps more with P1 than with N1 topography. The time windows are from 300 to 200 ms prestimulus (prestimulus total alpha activity), from 90 to 110 ms poststimulus (P1) and from 160 to 180 ms poststimulus (N1). All views are from the backside. Color bars indicate scales of amplitudes for total alpha activity, P1 and N1, respectively.

Figure 17 illustrates a potential explanation for the selective modulation of the P1 amplitude by prestimulus alpha dominance, which was absent for the N1 amplitude. Due to the time course of total alpha activity, the influence of ongoing alpha activity on ERP generation became weaker with time after stimulation.

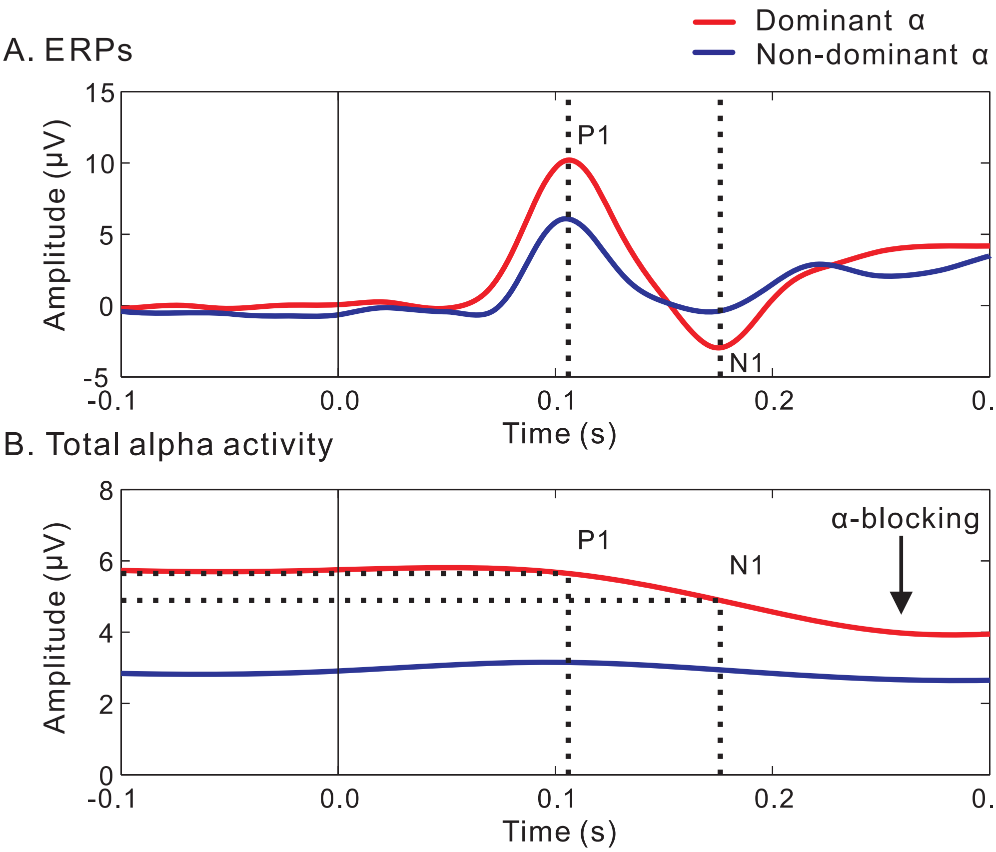


Figure 17. (A) Grand-averaged ERPs and (B) total alpha activity of individual alpha frequencies at electrode E59 in both groups (red lines: dominant alpha group, blue lines: non-dominant alpha group). Vertical dotted lines indicate the approximate latencies of P1 and N1 in the dominant alpha group, respectively. Notice that the level of total alpha activity is higher at the latency of P1 than N1, particularly in the dominant alpha group.

5.4. Discussion

P1 component

In the present study, the dominant alpha group showed higher P1 amplitudes than the non-dominant alpha group (cf. Figs. 15 and 16). Thus, it seems crucial for the modulation of early ERP components such as P1 whether or not prestimulus total alpha activity is dominant over the other frequency bands (except for the delta band as mentioned before). Such an increase of P1 amplitude depending upon prestimulus alpha dominance can hardly be explained by the traditional conceptions of the ERP which assume a poststimulus evoked response being additive to and independent of ongoing brain activity. Rather, our finding is in favor of phase-resetting of ongoing alpha activity or other non-linear interactions between ERPs and background activity. For instance, depending on the dominance of prestimulus ongoing alpha activity, a prompt poststimulus phase rearrangement of ongoing alpha activity might contribute to the generation of the P1. This interpretation is compatible with our previous observations about non-linear processes in ERP-generation (Study 1; Min et al., 2007). Moreover, Klimesch's group (Klimesch et al., 2004b; Gruber et al., 2005; Klimesch et al., 2007) proposed that phase-resetting of ongoing alpha activity may occur at around 100 ms (for visual stimuli), which is about the P1 latency. Recently, a study by Naruse et al. (2006) suggested such a 'phase-reset' mechanism for the alpha band by demonstrating a relationship between the alpha phase at stimulus onset and P1.

What remains to be shown is the functional meaning of such a modulation of the P1 component by the dominance of prestimulus alpha. The dominance of alpha activity has been related to vigilance (Johnson et al., 1969). Accordingly, the dominance of prestimulus alpha activity may be a prerequisite to effectively perform a cognitive task with a stimulus. Indeed, prestimulus alpha activity has been demonstrated to influence poststimulus processing (Nunn and Osselton, 1974; Varela et al., 1981; Ergenoglu et al., 2004; Hanslmayr et al., 2005).

In addition, it has been suggested that the momentary state of the brain, determining the response to a stimulus, may be reflected by the ongoing EEG (Basar, 1980b; Makeig et al., 2002; Barry et al., 2003; Makeig et al., 2004). Moreover, trial-by-trial fluctuations of event-related EEG signals have been demonstrated to reflect functionally significant changes in neural activity, for instance by predicting behavior on subsequent trials (Debener et al., 2005; Eichele et al., 2005; Debener et al., 2006; Benar et al., 2007), supporting the idea that the ongoing EEG comprises signals that influence the processing of event-related information (Makeig et al., 2004). Animal experiments also provide support for this assumption. Thus, for instance, it has been shown that low-frequency fluctuations in ongoing LFP activity account for a major part of the cortical response to visual stimuli in the cat (Arieli et al., 1996). Here we assume that the prestimulus alpha dominance at least partly reflects an activity state controlling the brain's momentary readiness for engaging in sensory or cognitive processes. Attention is one of the fundamental cognitive processes reflecting the brain's readiness for upcoming events. In line with this notion, studies have demonstrated that EEG alpha activity is associated with attentional mechanisms (Gomez et al., 1998; Klimesch et al., 1998; Klimesch, 1999; Herrmann and Knight, 2001; Sauseng et al., 2005b). Future studies are required investigating this issue in more detail by analyzing trial-by-trial changes of prestimulus alpha activity (Makeig et al., 2002).

N1 component

Our present study revealed that prestimulus alpha activity selectively modulates P1 but not N1 amplitude. As shown in Fig. 16, the topography of the N1 is different from that of the P1, suggesting that the underlying mechanisms of these two ERP components can be differentiated anatomically as well as functionally (Luck et al., 1990; Di Russo et al., 2002). The reduced influence of dominant prestimulus alpha activity on N1 probably reflects a decrease of the effect with increasing time after stimulus onset. As illustrated in Fig. 17, owing to the fast reduction in alpha activity just after stimulation (so-called 'alpha-blocking'), such a sudden suppression in poststimulus alpha amplitude might be the reason for affecting N1 less than P1. Trimble and Potts (1975) also attributed their similar findings to alpha-blocking. However, our present results do not rule out a modulation of N1 by the dominance of prestimulus alpha, as demonstrated previously (Makeig et al., 2002). Although in the present study none of the N1 effects reached statistical significance, the dominant alpha group yielded slightly larger N1 amplitudes than the non-dominant alpha group (Figs. 15, 16 and 17). It has been demonstrated that the visual N1 is enhanced for coherent Gestalt-like stimuli (Eimer and McCarthy, 1999; Herrmann and Bosch, 2001; Itier and Taylor, 2004; Ohla et al., 2005). Therefore, it might be speculated that our simple stimuli (circles and squares) were not ideally suited to evoke large N1 amplitudes and thus might have resulted in a weak relation to the prestimulus alpha dominance.

Behavioral results

There is evidence that the timing involved in perceptual gating is of the order of 100 ms and thus may be associated with the period of the alpha activity (Harter, 1967). Along the same line, Varela et al. (1981) proposed that alpha activity may be involved in perceptual timing processes. However, in the present study, reaction times and accuracy of task-performance did not appear to be associated with the dominance of prestimulus total alpha activity. One possible explanation is that our experimental tasks were too easy to uncover a modulation of behavioral responses in relation to the prestimulus alpha dominance. In addition, there is still some controversy over which attribute of alpha activity is related to behavior. For example, the alpha phase at stimulus onset has been suggested as a factor for controlling subsequent reaction times in both visual and auditory paradigms (Calloway and Yeager, 1960; Callaway, 1961; Dustman and Beck, 1965; Rice and Hagstrom, 1989). On the other hand, Michel et al. (1994) observed that reaction times significantly correlated with the duration of EEG or MEG alpha suppression. In addition, Surwillo (1964) suggested that individuals with higher alpha frequencies presented faster reaction times. He also attributed the variability in reaction times to the fact that the biological clock is not precise because the period of EEG waves varies from time to time (Surwillo, 1963). This variability could be attributed to differences in readiness, arousal variations, distraction or to shifts in attention. Therefore, a more thorough assessment of behavior in a more difficult task seems necessary to investigate the relationship between alpha EEG and behavioral control in future studies.

Conclusion

Dominance of prestimulus alpha activity seems to modulate early ERP-generation. The observed relationship between prestimulus alpha dominance and the amplitude of the visual P1 component can hardly be explained by the traditional ERP model, in which stimulation systematically adds an invariant response to ongoing activity, independent of prestimulus ongoing activity. Our results are consistent with phase-resetting of ongoing activity or other non-linear interactions between ERPs and background activity. This is generally in agreement with the recently proposed event-related brain dynamics model (Makeig et al., 2004). Early poststimulus alpha activity, as reflected in short latency ERP components, may be established at least partly by means of a partial reorganization of dominant prestimulus ongoing alpha activity.

Chapter 6: Prestimulus alpha activity and top-down function (Study 3)

The experimental results presented in this chapter are in press in the journal *Neuroscience Letters* (Min and Herrmann, in press).

6.1. Introduction

It has been reported that there is a substantial relationship between mental (cognitive) states and oscillatory brain activity (Basar, 1999b; Freeman, 2000; Basar et al., 2001). Moreover, it has been suggested that momentary states of the brain, determining the response to a stimulus, may be reflected in the ongoing EEG (Basar, 1980b; Basar et al., 1997; Barry et al., 2003). Since brain oscillations in the EEG alpha band (approximately 10 Hz) have been known as the most prominent brain oscillation present during relaxed wakefulness (Adrian and Matthews, 1934; Niedermeyer, 1999), spontaneous alpha activity most probably reflects a momentary mental state in relaxed wakefulness. Likewise, we supposed that top-down processing prior to stimulation would be reflected in the prestimulus ongoing alpha activity. In line with this view, we observed a significant relationship between prestimulus alpha dominance and P1 amplitude in favor of phase-resetting of ongoing alpha activity in Study 2 (Chapter 5). Since the early event-related potentials (ERPs) reflect stimulus-induced prompt brain responses, our findings suggested that the predominant ongoing alpha activity prior to stimulation might serve a certain purpose with respect to poststimulus mental processes. Klimesch et al. (2007) recently postulated that alpha synchronization might reflect a top-down function in inhibiting task-irrelevant information, since the event-related synchronization in the alpha band can be noticeably observed during task-performance either under such conditions where subjects have to withhold task-relevant information or over the brain regions that are task-irrelevant (Klimesch, 1999; Suffczynski et al., 2001; Jensen et al., 2002; Schack and Klimesch, 2002; Busch and Herrmann, 2003; Cooper et al., 2003; Herrmann et al., 2004c; Sauseng et al., 2005a). Therefore, by means of two kinds of discrimination tasks requiring inhibition of concurrent task-irrelevant feature processing for improving task-performance, here we would like to test a putative relationship between prestimulus EEG alpha dynamics and poststimulus responses of task-performance from the viewpoint of top-down inhibitory processing.

6.2. Materials and Methods

Subjects and experimental procedure

Sixteen subjects participated in this study (11 females, mean age 24; range 20-31 years). This research was carried out in accordance with local ethics guidelines and the Declaration of Helsinki (World Medical Association: Ethical Principles for Medical Research Involving Human Subjects, 1964). All subjects showed no signs of neurological or psychiatric disorders. All of them had normal or corrected-to-normal vision, and none of them were color-blind (examined by the *Ishihara* color test).

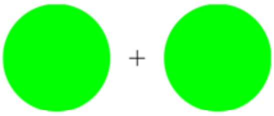
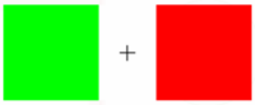
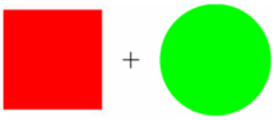
Samples of stimuli	Same shape	Different shape
Same color	 ('Identical' condition)	 ('Color-only' condition)
Different color	 ('Shape-only' condition)	 ('Neither' condition)

Figure 18. This schematic table shows four sample stimuli representing each stimulus-category. According to the presence or absence of identity of the two features color and shape, all stimuli are classified into 2x2 stimulus-categories.

Two stimuli randomly drawn from a set of red or green circles or squares (cf. Fig. 18) were presented bilaterally on a light-gray background at an eccentricity of 3° visual angle on a computer monitor, which was placed in front of the subject at a distance of 100 cm. Each stimulus spanned 4° visual angle for a duration of 700 ms. Stimulus presentation was followed by a variable inter-stimulus-interval ranging from 1300 to 1700 ms with a mean value of 1500 ms. The areas of circles and squares were matched and all types of stimuli appeared pseudo-randomly with equal probability. Prior to the experiment, we flickered red and green squares on the screen and instructed subjects to adjust the RGB values of the squares until the observed flickering was minimized. The resulting individual isoluminant RGB values for red and green were then used for the experiment.

In the main experiment, subjects were required to remain centrally fixated, and were instructed to press a button with the index finger of one hand if the task-relevant feature (‘color’ or ‘shape’ in a ‘color task’ and a ‘shape task’, respectively) was the same, and to press a button with the other hand if not. Since Mordkoff and Yantis (1993) reported that coactivation occurs when target attributes from two separable dimensions are simultaneously present, but not when target attributes come from the same dimension, here we employed two dimensions (color and shape) to induce such coactivation, requiring subjects to inhibit the task-irrelevant feature for improving performance. In order to analyze reaction times, subjects were asked to press the button as quickly as possible. Response hands and the sequence of presented tasks were counterbalanced across subjects. Stimuli in each task were presented in four blocks, separated by short rest periods in between.

Stimuli were classified according to whether the task-relevant or task-irrelevant feature (color or shape) of the bilaterally presented stimuli was the same or not. Consequently, we had four categories of stimulus-condition, as illustrated in Fig. 18. The ‘identical’ condition represented identical features in both color and shape dimensions across bilaterally presented stimuli. The ‘color-only’ condition consisted of a stimulus-type which showed identity only in the color-dimension. On the other hand, the ‘shape-only’ condition represented only shape-identical stimulus pairs. In the ‘neither’ condition, neither color nor shape were the same across the presented stimuli. The experiment consisted of 100 trials per stimulus-category, resulting in a total number of 400 trials for each task. Data were averaged within each stimulus-category and only trials with correct responses were further analyzed.

Data acquisition and analysis

EEG was recorded using a BrainAmp amplifier (Brain Products, Munich) with 32 sintered Ag/AgCl-electrodes mounted in an electrode cap (Easycap, Falk Minow Services, Munich) and placed according to the 10-10 system, with a nose-tip reference and ground electrode at AFz. Eye movement activity was monitored with an electrode placed sub-orbitally to the right eye and was referenced to the nose. Electrode impedances were maintained below 10 kΩ prior to data acquisition. EEG was analogue filtered from 0.016 to 250 Hz, digitized at 500 Hz and stored for off-line analysis. Recordings were made while subjects sat in a sound-attenuated and electrically shielded booth. Data were epoched from 500 ms before to 1000 ms after stimulus onset. Automatic artifact rejection excluded trials from further processing if the standard deviation within a moving 200 ms time interval exceeded 30 μV. Subsequently, all epochs were visually inspected for artifacts, and epochs containing eye-movements or electrode drifts were rejected.

For investigating the amplitude and time-course of oscillatory activity, the EEG signals were convolved with Morlet wavelets (Herrmann and Mecklinger, 2000; Herrmann et al., 2005). The wavelet transform was performed for each individual trial, and the absolute values of the resulting transforms were averaged. This measure reflects the 'total activity' for a certain frequency range, irrespective of whether it is phase-locked to the stimulus or not. Since activity in a prestimulus period would vanish after baseline correction, no baseline correction was applied to the total alpha activity.

It has been demonstrated that subjects differ considerably in their 'individual alpha frequency' (IAF; Doppelmayr et al., 1998b; Klimesch, 1999). Therefore, the frequencies used in the wavelet analyses of total alpha activity were determined individually for every subject. Time-frequency transforms for total activity were first computed for the electrode Pz, where the poststimulus amplitude modulation of alpha activity was most pronounced. From this time-frequency scalogram, the IAF was obtained as the maximum of total activity in the frequency range between 8 and 13 Hz in a time window from 400 to 200 ms prior to stimulus onset. For obtaining a single IAF irrespective of stimulus-categories and task-types, we averaged such maxima across all four stimulus-categories and both tasks within each subject. If there was no identifiable alpha peak (i.e. no local maximum) within such a time-frequency range, 10 Hz was selected as the IAF for those subjects. This had to be done for four subjects.

Reaction times were collected within their individual 95% confidence interval. The amplitude and latency of the P3 component were also evaluated. For the P3 analysis, we performed a baseline correction and assessed the maximum amplitude and latency of the P3 within the time window from 300 to 600 ms poststimulus. We analyzed all measures on the electrode Pz where poststimulus effects of both parieto-occipital alpha activity (Adrian and Matthews, 1934) and the P3 component (Polich et al., 1997) overlap and are most pronounced. In order to obtain the prestimulus total alpha activity, we measured mean values of the total alpha activity in the time window from 400 ms to 200 ms prestimulus. This time window was chosen to avoid the temporal smearing[21] of

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[21] Smearing is an artefact by wavelet transformation. The wavelet transformation considers multiple time points around the respective time point for convolution, and thus the peak width of the convolved signal will be smeared even into the baseline. Accordingly, the baseline should be

poststimulus activity into the baseline (Herrmann et al., 2005), and to include a reasonable period having more than one cycle of alpha frequency.

All measures were analyzed with a repeated measures ANOVA comprising two within-subjects factors labeled as ‘task’ (‘color task’ vs. ‘shape task’) and ‘condition’ (‘identical’ vs. ‘color-only’ vs. ‘shape-only’ vs. ‘neither’) and a between-subjects factor labeled as ‘task-order’ (‘color-first’ vs. ‘shape-first’). We introduced the sequence of presented tasks as a between-subjects factor in order to check whether task-shifting between experimental blocks influences task-performance. The Greenhouse-Geisser correction was used where appropriate. To analyze subjects’ experience during the task, a short interview was additionally performed after the experiment.

6.3. Results

We observed that the reaction times of the color task were significantly shorter than those of the shape task (F(1,14)= 44.222, *p*<.0005; cf. Fig. 19C). There was also a significant ‘condition’ effect (F(3,42)= 17.624, *p*<.0005) and a significant interaction effect on reaction times (‘task’ x ‘condition’: F(3,42)= 14.342, *p*<.0005). For the P3 amplitude, we found a strong ‘condition’ effect (F(3,42)= 25.157, *p*<.0005) and a significant interaction effect (‘task’ x ‘condition’: F(3,42)= 8.611, *p*<.0005), but no significant ‘task’ effect (F(1,14)= 2.159, *ns*). As for the P3 latency, there were main effects of both ‘task’ (F(1,14)= 44.247, *p*<.0005; cf. Fig. 19B) and ‘condition’ (F(3,42)= 9.392, *p*<.0005). The interaction effect between them also turned out to be significant (F(3,42)= 10.210, *p*<.0005).

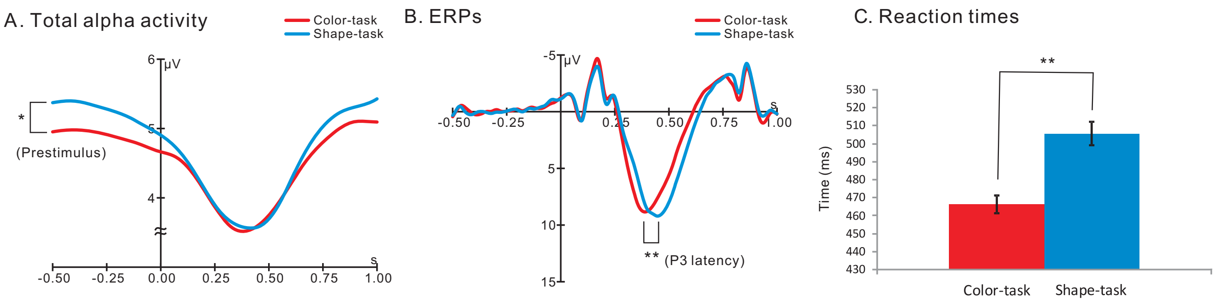

Figure 19. (A) Grand-averaged time courses of total alpha activity at electrode Pz, (B) grand-averaged ERPs at electrode Pz and (C) a bar graph of reaction times. These data are averaged across four categories of stimulus-condition in both tasks. Red lines (or a red bar) indicate the color task and blue lines (or a blue bar) the shape task. In (C), error bars represent ±1 standard error of the mean. For display of ERPs, we performed a 20 Hz low-pass filtering. Notice the

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chosen to fairly precede the stimulation.

significant differences indicated by brackets: prestimulus levels of total alpha activity in (A); P3 latencies in (B); reaction times in (C). The number of asterisks indicates levels of statistical significance: * indicates *p*<0.01, and ** indicates *p*<0.0005.

We found that the shape task was preceded by significantly higher prestimulus total alpha amplitudes than the color task (F(1,14)= 5.024, *p*<.05; color task: 4.9 μV; shape task: 5.3 μV; cf. Fig. 19A). In addition, we noted a significant interaction ('task' x 'task-order': F(1,14)= 6.384, *p*<.05). No other main effects or interactions yielded significant results.

6.4. Discussion

The shape task yielded significantly longer reaction times and P3 latencies as well as higher amplitudes of *prestimulus* total alpha activity than the color task (cf. Fig. 19). These findings suggest that the prestimulus alpha activity seems to have a functional relationship with reaction time and P3 latency. Since modulation of reaction times and P3 are considered to be indicative of different efficiencies in information processing (McCarthy and Donchin, 1981; Duncan-Johnson and Donchin, 1982; Pfefferbaum et al., 1983), our findings indicate that the shape task is more difficult than the color task. As the shape task resulted in longer reaction times than the color task, the color feature seemed more salient than the shape feature. In the shape task, subjects should inhibit perceptual processing of the color feature for improving task-performance, and vice versa in the color task. Presumably, subjects prepared an adequate mental state for inhibition before stimulation. If enhancement of alpha activity reflects a top-down inhibitory control as Klimesch et al. (2007) suggested, the higher prestimulus alpha amplitude in the shape task than the color task implies that more inhibition is necessary for performing the shape task in advance of stimulation. That is, suppressing the perceptual processing of the color feature in the shape task requires more prestimulus alpha activity. Since the color feature is more salient than the shape feature, it seems plausible to assume that inhibiting the salient color feature requires more alpha activity prior to stimulation in order to perform the upcoming shape task efficiently. This interpretation of the prestimulus alpha activity is in line with Klimesch's inhibition hypothesis (Klimesch et al., 2007).

A number of studies reported that prestimulus alpha activity modulates poststimulus ERPs (Jasiukaitis and Hakerem, 1988; Haig and Gordon, 1998a; Ergenoglu et al., 2004). This indicates that prestimulus alpha activity can influence poststimulus cognitive processing, which we will consider the weak hypothesis about prestimulus alpha activity. Even more interestingly, it has been demonstrated that the alpha phase at stimulus onset or prior to stimulus onset modulates human reaction time (Calloway and Yeager, 1960; Callaway, 1961; Dustman and Beck, 1965; Rice and Hagstrom, 1989; Haig and Gordon, 1998b). This indicates that prestimulus alpha activity even influences human performance, which we will consider the strong hypothesis about prestimulus alpha activity. Our data show that prestimulus alpha activity influences reaction time as well as P3 latency. Since P3 latency is closely related to reaction time (Verleger, 1997), our findings support the strong hypothesis about prestimulus alpha activity. In conclusion, our data together with previous findings support the notion that prestimulus alpha activity can influence both poststimulus cognitive processing and even the manual response that results from this processing. Such a prestimulus alpha influence on the poststimulus performance implies that prestimulus alpha activity reflects a top-down preparatory mental state for upcoming task-performance.

Chapter 7: Summary and General Discussion

In order to evaluate the functional significance of ongoing alpha activity, the present thesis consists of three studies on ongoing dynamics of alpha activity in relation to ERP-generation, as well as its putative function with respect to top-down processing. The characteristically pronounced prestimulus alpha activity over the other frequency bands offer a favorable condition for estimating the phase-reset model, which allows us to validate the functional importance of 'ongoing' activity, the subject of Study 1. Following this study, in Study 2 I examined the dependency of the subsequent ERP components on prestimulus alpha dominance. Finally, in Study 3 I attempted to investigate a putative function of prestimulus alpha activity in relation to top-down processing. After all, the present thesis might provide a more plausible understanding of alpha contribution to the ERP-generation from the viewpoint of phase-resetting as well as its reflection of top-down processing.

7.1. Summary of the experimental results

It is noteworthy that in some subjects the prestimulus alpha activity is more pronounced than in the others. Using this inter-individual variability, Study 1 (Chapter 4) demonstrated different poststimulus EEG alpha dynamics according to the amount of prestimulus alpha activity. In order to validate the two established models for ERP-generation (i.e. phase-resetting and additive-power), we investigated poststimulus EEG alpha dynamics in terms of the dissociable total and evoked activity. Despite the results of accompanying poststimulus dynamics between both activity in the alpha band (i.e., concurrent increment in both), a complementary simulation analysis suggested that both phase-resetting and additive-power can coexist after stimulation.

Through Study 2 (Chapter 5), we observed enhanced P1 amplitudes, particularly in individuals with dominant prestimulus alpha activity rather than those without dominant prestimulus alpha activity. Such poststimulus reflection of a prestimulus alpha attribute suggests that P1 is generated at least partly by the reorganization of ongoing alpha activity. Thus, an attribute (dominance) of prestimulus alpha is reflected in poststimulus ERP-modulation. These observations also provide considerable evidence for involvement of phase-resetting in ERP-generation.

In favor of functional significance of prestimulus alpha activity, we found that differences in prestimulus alpha activity yielded differences in poststimulus task-performance in Study 3 (Chapter 6). To interpret these observations, we supposed that prestimulus alpha activity might reflect a top-down control for preparing subsequent task-performance. Since we also observed the 'task' effect in reaction times and in P3 latencies, prestimulus alpha seems to predict such poststimulus responses. Consequently, prestimulus alpha activity probably reflects top-down preparations prior to stimulation and modulates subsequent poststimulus responses.

7.2. Dynamics and function of ongoing alpha activity

On the basis of the three studies in this thesis, it is suggested that both partial phase-resetting and partial additive power contribute to ERP-generation at least in the alpha band, and that prestimulus alpha activity reflects prestimulus top-down information. Through Study 2, the significant influence of a prestimulus alpha attribute (dominance) on the subsequent ERP generation reinforces the functional importance of reorganization of 'ongoing' alpha activity. Taken together with the findings in Study 2, the results in Study 3 propose that poststimulus interaction between ongoing top-down processing and incident bottom-up stimulation around P1 latency may be reflected in poststimulus reorganization of ongoing alpha activity, which may already convey prestimulus top-down preparations for performing a subsequent task. This view is in line with the recent suggestion by Klimesch et al. (2007). They proposed that event-related alpha coherence emerges at P1 latency when, they assumed, the earliest manifestation of a top-down process may influence bottom-up sensory processing, since it was observed that P1 reflects the timing of early categorization processes (Hanslmayr et al., 2005) and the timing of coactivation between brain areas during interactive top-down and bottom-up processing (Schack et al., 2003).

In Study 1, it was proposed that both phase-resetting and additive-power are evenly plausible within the alpha frequency range. In agreement with this view, a visual study by Kirschfeld (2005) proposed that EEG alpha activity comprises both linear and nonlinear components. According to his report, the linear component resulted from flash-evoked potentials, which are superimposed on ongoing alpha oscillations without phase-resetting. On the other hand, light-adaptation yielded the nonlinear component, which is most likely presumed as phase-resetting. Likewise, an auditory study by Fuentemilla et al. (2006) suggested that both models are plausible, depending on the stimulation condition. They found that the 'additive power' model was most likely to explain responses to the first presented stimulus but phase-resetting was a more plausible mechanism when stimuli were presented as second or third in a row. Taken together, an integrative interpretation of the above studies and ours is that the poststimulus dynamics of the alpha band depends upon the prestimulus brain condition with respect to mental events.

Furthermore, both studies by Kirschfeld (2005) and by Fuentemilla et al. (2006) demonstrated that a kind of adaptive mental condition by repetitive stimulation yields considerable evidence in favor of phase-resetting. Adaptation established by repeated stimulation may constitute a temporal neuronal network for enhancing response-efficiency to experienced and expected stimulation. Then, ongoing oscillations within such a neural coalition by adaptation are more likely self-reorganized by familiar stimulation. Presumably through this method, a top-down control is available from higher processing stages to primary processing stages within such a neural assembly.

Even in animal studies, such a top-down control was reported in terms of either coherence or synchronization in the alpha frequency range. In the rat brain, Nicolelis and Fanselow (2002) observed that large-scale coherent alpha activity appears first in the sensory cortex and later in the thalamus (VPM) during the whisker-twitching state. During this state, a rat seems to be in a state of expectant attention in which an environmental change is predicted, and thus the cortex may initiate a top-down process to facilitate the encoding of a stimulus when it occurs (Klimesch et al., 2007), because rats use their whiskers to encode tactile information. In addition, von Stein et al. (2000) observed synchronization of alpha oscillations between primary and higher visual areas in the cat brain. In response only to familiar stimuli, alpha activity showed a prominent latency shift between higher and primary brain areas in a way of a top-down directed interaction.

Therefore, the ongoing alpha activity prior to experienced stimulation most likely mediates top-down influence on subsequent familiar information processing. This interpretation is also based on the observations in Study 3, since different types of repetitive acquainted tasks were reflected in differences in prestimulus alpha activity. In other words, prestimulus alpha activity seems to be involved in preliminary stimulus-processing stages preparing subsequent task-performance. Babiloni et al. (2006b) consistently reported that visual consciousness highly covaries with prestimulus cortical alpha rhythms. Their results are in line with previous EEG evidence that a better cognitive performance is predicted by higher prestimulus alpha power (Klimesch, 1997, 1999; Klimesch et al., 2003). It seems that the stronger the prestimulus alpha activity, the stronger its activity reduction during the stimulus processing and the better the cognitive performance owing to a well-prepared mental state for upcoming task-performance presumably being reflected in enhanced prestimulus alpha activity.

As mentioned in Section 1.3, Shaw (1996) suggested that alpha enhancement relates more generally to *intention*, which can be defined as involving cognitive processes that precede any action, whether or not it involves motor activity (Brand, 1984). Together with such a viewpoint of *intention* in a paradigm of careful movement (Shaw, 1996), I propose that a concentrated mental attitude to process upcoming information results in enhancement of alpha activity. This is because withholding a mental preparatory state to perform a subsequent task and controlling the execution of careful movement are both utilized by means of an internally concentrated mental state. As mentioned earlier, on the cellular level such a concentrated mental state can be accomplished through constructing (or holding)[22] an assembly of task-relevant neurons. These neurons seem to activate together in advance of the occurrence of events (stimulus or action) to facilitate upcoming information processes. Here I surmise that strengthening this neural network in a top-down manner leads to enhancement in alpha activity. Within this framework, to some extent, we are also able to understand a paradoxical increase in alpha under particular conditions where subjects have to withhold task-relevant information or over the brain regions that are task-irrelevant (Klimesch, 1999; Suffczynski et al., 2001; Jensen et al., 2002; Schack and Klimesch, 2002; Cooper et al., 2003; Herrmann et al., 2004c; Sauseng et al., 2005a). This may occur together with active suppression of an information flow irrelevant to the current mental topic in working memory (Jensen et al., 2002; Sauseng et al., 2005a; Klimesch et al., 2007).

Other experimental observations reinforce the role of alpha activity, among all frequency bands, as the most probable carrier of a top-down control. Since it has been reported that global binding of local networks is accomplished at human alpha frequency[23] (Mima et al., 2001; Nunez et al., 2001; Sauseng et al., 2005a), alpha synchronization appears to be crucially involved in top-down processing. Additionally, as mentioned in Section 1.3, multistable stimuli enable us to investigate visual awareness in

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[22] This is because pronounced ERS in the alpha band can be observed during an information-encoding or retention phase, not an information-retrieval phase (Schack et al., 2005; Klimesch et al., 2007).

[23] So-called ‘traveling waves’ have been observed in event-related alpha dynamics on the scalp. Traveling alpha waves may reflect spreading cortical activation moving from one brain region to another in a top-down manner, e.g. from anterior to posterior sites (Sauseng et al., 2005a).

a top-down fashion[24]. Although multistable perception has mainly been reported in relation to reduction in alpha activity (Isoglu-Alkac et al., 2000) as well as enhancement in gamma activity (Basar-Eroglu et al., 1996; Strüber et al., 2001), Strüber and Herrmann (2002) reported that it is not gamma, but alpha activity that reflects significant differences between endogenous and exogenous reversals by means of an ambiguous motion paradigm. In addition to these findings, they observed changes in the endogenous alpha activity preceding the reversal phase, which is consistent with the results in Study 3.

7.3. Perspectives for future research

Although the functional significance of prestimulus alpha activity is noteworthy as such, it has only recently been highlighted. This is probably because traditional EEG studies have employed a method of baseline correction for general EEG analysis without any caution even in the alpha band, which typically demonstrates pronounced amplitudes in the baseline period. Therefore, the observations of poststimulus alpha-decrease in some baseline-corrected studies should be potentially reinterpreted another way; their results might not simply indicate a poststimulus alpha-decrease, but rather an actual alpha-increase already before stimulation. Indeed, the measures of ERD and ERS deal with prestimulus values without baseline correction. However, they are all computed as a ratio relative to their poststimulus changes. Thus, in this dissertation project, in order to evaluate the significance of pure prestimulus alpha activity, I focused only on prestimulus alpha activity without baseline correction. In addition to this point, I would like to address several plausible questions open for future research as follows.

Firstly, although alpha activity is the most ubiquitous component of the EEG, EEG activity in other frequency bands is also associated with mental events. While the present study provides considerable evidence for a top-down function in the alpha band, the functional relationship between alpha activity and the other oscillations needs further study in relation to information processing. For example, Herrmann et al. (2004a) proposed a match between top-down and bottom-up processes in the early evoked gamma activity around 80-100 ms poststimulus. Consistent with the time range of the memory match in their model, Study 2 suggests a putative interaction between top-down

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[24] There is another approach for the explanation of reversible figures, which emphasizes more passive (or bottom-up) processes of neural satiation or fatigue and recovery among cortical structures (Babich and Standing, 1981; Long et al., 1992). Although both approaches are controversial, in the present thesis I prefer to adopt the top-down approach for understanding reversible perception.

and bottom-up processing, which may be reflected in the reorganization of ongoing alpha activity around P1 latency (i.e., approximately 100 ms poststimulus). Accordingly, gamma activity seems to be functionally associated with alpha activity in information processing. For instance, Sewards and Sewards (1999) proposed a functional relation between alpha and gamma activity in visual awareness. Since they supposed that moving objects are represented by phase-correlated alpha and gamma activity and static objects are represented exclusively by phase-correlated alpha oscillations, they suggested that alpha activity occurs in the parvocellular pathway, whereas gamma activity occurs in the magnocellular pathway, and that two modes of oscillation are correlated. This hypothesis is worth evaluating in future research, to shed light on cognitive functional relationships between different frequency bands[25].

Secondly, in the present thesis, we analyzed our data on the categorized-subject level. Namely, we first categorized subjects according to the averaged amount or dominance of prestimulus alpha activity and then compared the group-averaged measures. Although such between-subjects design is able to investigate representative characteristics averaged across all trials on the subject level, if one assesses prestimulus alpha activity in a single trial level, it may account better for the within-subject variances in prestimulus alpha activity. Moreover, such variances in prestimulus alpha activity from condition to condition may indicate a critical mental state, which reflects an aspect of the brain's momentary readiness state that influences the subsequent sensory or cognitive processes[26]. In fact, there are several studies that employ the trial-by-trial analysis on prestimulus alpha activity, but they primarily analyzed the modulation of ERP components (Basar, 1980b; Basar and Stampfer, 1985; Brandt et al., 1991; Brandt and Jansen, 1991; Jansen and Brandt, 1991; Rahn and Basar, 1993a, b; Brandt, 1997; Barry et al., 2000). Thus, the trial-by-trial analysis in relation to top-down processing is one of the other

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[25] Recently, colleagues in our laboratory observed that evoked gamma activity was strongest for the low spatial frequency of stimulus property, whereas alpha activity was strongest for the high spatial frequency. They proposed that these results might link evoked and induced alpha and evoked gamma activity in human EEG to different modes of stimulus processing (Fründ et al. in press).

[26] There are a variety of studies that suggest alpha phase is related to different perception (Nunn and Osselton, 1974; Varela et al., 1981) and behavioral measures (Calloway and Yeager, 1960; Dustman and Beck, 1965; Rice and Hagstrom, 1989). Thus, in case of trial-by-trial analyses, taking alpha phase into consideration may also provide more information about the function of alpha activity in information processing.

prospective ways to estimate the brain’s momentary function that seems to be reflected at least in ongoing alpha activity.

Thirdly, nevertheless, there are some limitations of the work on the EEG and psychological processes. For example, as recounted in Section 2.1, the conventional EEG is mostly sampling the electrical activity of the cortex. However, a lot of information processing also occurs in sub-cortical structures. For instance, Smith et al. (1999) showed that changes occur in information processing such that novel tasks involve large areas of brain, but as tasks become more familiar, brain activity becomes more restricted and increasingly involves sub-cortical centers. Accordingly, not only neuroimaging techniques such as EEG and fMRI, but also local field potentials (LFPs) or cell-recordings on deep structures should be accompanied for further investigation into the issues of cognitive science in future research.

7.4. Conclusion

Through this dissertation project, I attempted to understand the functional dynamics of ongoing alpha activity and its relation to mental events. Study 1 demonstrated the existence of an additive power by stimulation in all groups irrespective of the amount of prestimulus alpha activity, while Study 2 provided considerable evidence in favor of phase-resetting of ongoing alpha activity in ERP-generation within the same data set as Study 1. In addition, Study 3 proposed that prestimulus alpha activity probably reflects top-down inhibitory processing in advance of stimulation and modulates subsequent poststimulus responses. To sum up, it seems that the ‘phase-reset’ and the ‘additive power’ models for ERP-generation are evenly plausible within a single framework and able to coexist. Furthermore, prestimulus ongoing EEG activity presumably reflects our mental state prior to stimulation. These phenomena were observed, at least in the EEG alpha band, through the present project.

Bibliography

Adrian ED, Matthews BHC (1934) The Berger rhythm: Potential changes from the occipital lobes in man. Brain 57:355-385.

Adrian ED (1944) Brain rhythms. Nature 153:360-362.

Andersen P, Andersson SA (1968) Physiological basis of the alpha rhythm. New York: Appelton Century Crofts.

Arieli A, Sterkin A, Grinvald A, Aertsen A (1996) Dynamics of ongoing activity: explanation of the large variability in evoked cortical responses. Science 273:1868-1871.

Babich S, Standing L (1981) Satiation effects with reversible figures. Percept Mot Skills 52:203-210.

Babiloni C, Brancucci A, Del Percio C, Capotosto P, Arendt-Nielsen L, Chen AC, Rossini PM (2006a) Anticipatory electroencephalography alpha rhythm predicts subjective perception of pain intensity. J Pain 7:709-717.

Babiloni C, Vecchio F, Bultrini A, Luca Romani G, Rossini PM (2006b) Pre- and poststimulus alpha rhythms are related to conscious visual perception: a high-resolution EEG study. Cereb Cortex 16:1690-1700.

Barry RJ, Kirkaikul S, Hodder D (2000) EEG alpha activity and the ERP to target stimuli in an auditory oddball paradigm. Int J Psychophysiol 39:39-50.

Barry RJ, Hodder D, Clarke AR, Johnstone SJ, De Pascalis V (2003) Preferred EEG brain states at stimulus onset in a fixed interstimulus interval auditory oddball task, and their effects on ERP components. Int J Psychophysiol 47:187-198.

Basar E (1980a) EEG-Brain Dynamics: Relation Between EEG and Brain Evoked Potentials. In, p 411. New York: Elsevier.

Basar E (1980b) EEG-Brain Dynamics: Relation Between EEG and Brain Evoked Potentials. In, pp 375-391. New York: Elsevier.

Basar E, Stampfer HG (1985) Important associations among EEG-dynamics, event-related potentials, short-term memory and learning. Int J Neurosci 26:161-180.

Basar E, Schürmann M, Basar-Eroglu C, Karakas S (1997) Alpha oscillations in brain functioning: an integrative theory. Int J Psychophysiol 26:5-29.

Basar E (1999a) Brain function and oscillations. Vol. I: Principles and approaches. Berlin: Springer.

Basar E (1999b) Brain function and oscillations. Vol. II: Integrative brain function, neurophysiology and cognitive processes. Berlin: Springer.

Basar E, Basar-Eroglu C, Karakas S, Schürmann M (1999) Oscillatory brain theory: a new trend in neuroscience. IEEE Eng Med Biol Mag 18:56-66.

Basar E, Basar-Eroglu C, Karakas S, Schürmann M (2001) Gamma, alpha, delta, and theta oscillations govern cognitive processes. Int J Psychophysiol 39:241-248.

Basar-Eroglu C, Basar E, Demiralp T, Schürmann M (1992) P300-response: possible psychophysiological correlates in delta and theta frequency channels. A review. Int J Psychophysiol 13:161-179.

Basar-Eroglu C, Strüber D, Kruse P, Basar E, Stadler M (1996) Frontal gamma-band enhancement during multistable visual perception. Int J Psychophysiol 24:113-125.

Basar-Eroglu C, Demiralp T (2001) Event-related theta oscillations: An integrative and comparative approach in the human and animal brain. Int J Psychophysiol 39:167-195.

Benar CG, Schon D, Grimault S, Nazarian B, Burle B, Roth M, Badier JM, Marquis P, Liegeois-Chauvel C, Anton JL (2007) Single-trial analysis of oddball event-related potentials in simultaneous EEG-fMRI. Hum Brain Mapp [Epub ahead of print].

Berger H (1929) Über das Elektrenkephalogramm des Menschen. Archiv für Psychiatrie und Nervenkrankheiten 87:527-570.

Brand M (1984) Intending and acting: Toward a naturalized action theory. In, p 296. Cambridge, MA: The MIT press.

Brandt ME, Jansen BH, Carbonari JP (1991) Pre-stimulus spectral EEG patterns and the visual evoked response. Electroencephalogr Clin Neurophysiol 80:16-20.

Brandt ME, Jansen BH (1991) The relationship between prestimulus-alpha amplitude and visual evoked potential amplitude. Int J Neurosci 61:261-268.

Brandt ME (1992) Topographic mapping of brain electromagnetic signals: a review of current technology. Am J Physiol Imaging 7:160-174.

Brandt ME (1997) Visual and auditory evoked phase resetting of the alpha EEG. Int J Psychophysiol 26:285-298.

Bressler SL (1995) Large-scale cortical networks and cognition. Brain Res Rev 20:288-304.

Busch NA, Herrmann CS (2003) Object-load and feature-load modulate EEG in a short-term memory task. Neuroreport 14:1721-1724.

Busch NA, Debener S, Kranczioch C, Engel AK, Herrmann CS (2004) Size matters: effects of stimulus size, duration and eccentricity on the visual gamma-band response. Clin Neurophysiol 115:1810-1820.

Callaway E (1961) Day-to-day variability in relationship between electroencephalographic alpha phase and reaction time to visual stimuli. Ann N Y Acad Sci 92:1183-1186.

Calloway E, Yeager CL (1960) Relationship between reaction time and electroencephalographic alpha phase. Science 132:1765-1766.

Cantero JL, Atienza M, Gomez C, Salas RM (1999) Spectral structure and brain mapping of human alpha activities in different arousal states. Neuropsychobiology 39:110-116.

Caton R (1875) The electric currents of the brain. Br Med J 2:278.

Celesia GG, Peachey NS, Brigell M, DeMarco PJ, Jr. (1996) Visual evoked potentials: recent advances. Electroencephalogr Clin Neurophysiol Suppl 46:3-14.

Chapman RM, Shelburne SA, Jr., Bragdon HR (1970) EEG alpha activity influenced by visual input and not by eye position. Electroencephalogr Clin Neurophysiol 28:183-189.

Chen Z, Tretyakov A, Takayasu H, Nakasato N (1998) Spectral analysis of multichannel meg data. Fractals 6:395-400.

Coenen A, Zajachkivsky O, Bilski R (1998) In the footsteps of Beck: the desynchronization of the electroencephalogram. Electroencephalogr Clin Neurophysiol 106:330-335.

Cooper NR, Croft RJ, Dominey SJ, Burgess AP, Gruzelier JH (2003) Paradox lost? Exploring the role of alpha oscillations during externally vs. internally directed attention and the implications for idling and inhibition hypotheses. Int J Psychophysiol 47:65-74.

Cooper NR, Burgess AP, Croft RJ, Gruzelier JH (2006) Investigating evoked and induced electroencephalogram activity in task-related alpha power increases during an internally directed attention task. Neuroreport 17:205-208.

Cooper R, Winter AL, Crow HJ, Walter WG (1965) Comparison of Subcortical, Cortical and Scalp Activity Using Chronically Indwelling Electrodes in Man. Electroencephalogr Clin Neurophysiol 18:217-228.

Davis H, Davis PA (1936) Active potentials of the brain in normal persons and in normal states of cerebral activity. Arch Neurol Psychiatry 36:1214-1224.

Debener S, Herrmann CS, Kranczioch C, Gembris D, Engel AK (2003) Top-down attentional processing enhances auditory evoked gamma band activity. Neuroreport 14:683-686.

Debener S, Ullsperger M, Siegel M, Fiehler K, von Cramon DY, Engel AK (2005) Trial-by-trial coupling of concurrent electroencephalogram and functional magnetic resonance imaging identifies the dynamics of performance monitoring. J Neurosci 25:11730-11737.

Debener S, Ullsperger M, Siegel M, Engel AK (2006) Single-trial EEG-fMRI reveals the dynamics of cognitive function. Trends Cogn Sci 10:558-563.

Delorme A, Makeig S (2004) EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. J Neurosci Methods 134:9-21.

DeLucchi MR, Garoutte B, Aird RB (1962) The scalp as an electroencephalographic averager. Electroencephalogr Clin Neurophysiol 14:191-196.

Demiralp T, Ademoglu A (2001) Decomposition of event-related brain potentials into multiple functional components using wavelet transform. Clin Electroencephalogr 32:122-138.

Demiralp T, Bayraktaroglu Z, Lenz D, Junge S, Busch NA, Maess B, Ergen M, Herrmann CS (2006) Gamma amplitudes are coupled to theta phase in human EEG during visual perception. Int J Psychophysiol [Epub ahead of print].

Deuschl G, Eisen A (1999) Recommendations for the practice of clinical neurophysiology. Clin Neurophysiol:304.

Di Russo F, Martinez A, Sereno MI, Pitzalis S, Hillyard SA (2002) Cortical sources of the early components of the visual evoked potential. Hum Brain Mapp 15:95-111.

Donchin E (1979) Event-related brain potentials in the study of human information processing. In: Evoked brain potentials and behaviour (Begleiter H, ed), pp 13-88. New York: Plenum Press.

Donchin E, Coles MGH (1988) Is the P300 component a manifestation of context updating? Behav Brain Sci 11:357-374.

Doppelmayr M, Klimesch W, Pachinger T, Ripper B (1998a) The functional significance of absolute power with respect to event-related desynchronization. Brain Topogr 11:133-140.

Doppelmayr M, Klimesch W, Pachinger T, Ripper B (1998b) Individual differences in brain dynamics: important implications for the calculation of event-related band power. Biol Cybern 79:49-57.

Doppelmayr M, Klimesch W, Sauseng P, Hödlmoser K, Stadler W, Hanslmayr S (2005a) Intelligence related differences in EEG-bandpower. Neuroscience Letters 381:309-313.

Doppelmayr M, Klimesch W, Hödlmoser K, Sauseng P, Gruber W (2005b) Intelligence related upper alpha desynchronization in a semantic memory task. Brain Research Bulletin 66:171-177.

Duncan-Johnson CC, Donchin E (1982) The P300 component of the event-related brain potential as an index of information processing. Biol Psychol 14:1-52.

Dustman RE, Beck EC (1965) Phase of Alpha Brain Waves, Reaction Time and Visually Evoked Potentials. Electroencephalogr Clin Neurophysiol 18:433-440.

Earle JB (1988) Task difficulty and EEG alpha asymmetry: an amplitude and frequency analysis. Neuropsychobiology 20:95-112.

Edgar JC, Stewart JL, Miller GA (2005) Digital filters in ERP research. In: Event-related potentials: a methods handbook (Handy TC, ed), pp 85-113. Cambridge: The MIT press.

Eichele T, Specht K, Moosmann M, Jongsma ML, Quiroga RQ, Nordby H, Hugdahl K (2005) Assessing the spatiotemporal evolution of neuronal activation with single-trial event-related potentials and functional MRI. Proc Natl Acad Sci U S A 102:17798-17803.

Eimer M, McCarthy RA (1999) Prosopagnosia and structural encoding of faces: evidence from event-related potentials. Neuroreport 10:255-259.

Ellingson RJ (1956) Brain waves and problems of psychology. Psychol Bull 53:1-34.

Engel AK, Fries P, Singer W (2001) Dynamic predictions: oscillations and synchrony in top-down processing. Nat Rev Neurosci 2:704-716.

Ergenoglu T, Demiralp T, Bayraktaroglu Z, Ergen M, Beydagi H, Uresin Y (2004) Alpha rhythm of the EEG modulates visual detection performance in humans. Cogn Brain Res 20:376-383.

Fell J, Klaver P, Elfadil H, Schaller C, Elger CE, Fernandez G (2003) Rhinal-hippocampal theta coherence during declarative memory formation: interaction with gamma synchronization? Eur J Neurosci 17:1082-1088.

Fell J, Dietl T, Grunwald T, Kurthen M, Klaver P, Trautner P, Schaller C, Elger CE, Fernandez G (2004) Neural bases of cognitive ERPs: more than phase reset. J Cogn Neurosci 16:1595-1604.

Ferree TC, Luu P, Russell GS, Tucker DM (2001) Scalp electrode impedance, infection risk, and EEG data quality. Clin Neurophysiol 112:536-544.

Ferree TC (2006) Spherical splines and average referencing in scalp electroencephalography. Brain Topogr 19:43-52.

Fingelkurts AA, Fingelkurts AA, Krause CM, Sams M (2002) Probability interrelations between pre-/post-stimulus intervals and ERD/ERS during a memory task. Clinical Neurophysiology 113:826-843.

Freeman WJ (2000) Mesoscopic neurodynamics: from neuron to brain. J Physiol Paris 94:303-322.

Freeman WJ, Burke BC, Holmes MD (2003) Aperiodic phase re-setting in scalp EEG of beta-gamma oscillations by state transitions at alpha-theta rates. Hum Brain Mapp 19:248-272.

Freeman WJ (2006) Origin, structure, and role of background EEG activity. Part 4: Neural frame simulation. Clin Neurophysiol 117:572-589.

Fründ I, Busch NA, Körner U, Schadow J, Herrmann CS (in press) EEG oscillations in the gamma and alpha range respond differently to spatial frequency. Vision Res.

Fuentemilla L, Marco-Pallares J, Grau C (2006) Modulation of spectral power and of phase resetting of EEG contributes differentially to the generation of auditory event-related potentials. Neuroimage 30:909-916.

Galambos R (1992) A comparison of certain gamma band (40Hz) brain rhythms in cat and man. In: Induced rhythms in the brain (Basar E, Bullock T, eds), pp 201-216. Boston: Birkhauser.

Gevins A, Leong H, Smith ME, Le J, Du R (1995) Mapping cognitive brain function with modern high-resolution electroencephalography. Trends Neurosci 18:429-436.

Goldman RI, Stern JM, Engel J, Jr., Cohen MS (2000) Acquiring simultaneous EEG and functional MRI. Clin Neurophysiol 111:1974-1980.

Golla F, Hutton EL, Walter WG (1943) The objective study of mental imagery. I. Physiological concomitants. J Ment Sci 89:216-223.

Gomez CM, Vazquez M, Vaquero E, Lopez-Mendoza D, Cardoso MJ (1998) Frequency analysis of the EEG during spatial selective attention. Int J Neurosci 95:17-32.

Goodman DM (1976) The effect of oculomotor activity on alphablocking in the absence of visual stimuli. Psychophysiology 13:462-465.

Grabner RH, Fink A, Stipacek A, Neuper C, Neubauer AC (2004) Intelligence and working memory systems: Evidence of neural efficiency in alpha band ERD. Cogn Brain Res 20:212-225.

Gregory RL (1998) The oxford companion to THE MIND. Oxford: Oxford University Press.

Gruber WR, Klimesch W, Sauseng P, Doppelmayr M (2005) Alpha Phase Synchronization Predicts P1 and N1 Latency and Amplitude Size. Cereb Cortex 15:371-377.

Haig AR, Gordon E (1998a) EEG alpha phase at stimulus onset significantly affects the amplitude of the P3 ERP component. Int J Neurosci 93:101-115.

Haig AR, Gordon E (1998b) Prestimulus EEG alpha phase synchronicity influences N100 amplitude and reaction time. Psychophysiology 35:591-595.

Hanslmayr S, Klimesch W, Sauseng P, Gruber W, Doppelmayr M, Freunberger R, Pecherstorfer T (2005) Visual discrimination performance is related to decreased alpha amplitude but increased phase locking. Neurosci Lett 375:64-68.

Hanslmayr S, Klimesch W, Sauseng P, Gruber W, Doppelmayr M, Freunberger R, Pecherstorfer T, Birbaumer N (2007) Alpha phase reset contributes to the generation of ERPs. Cereb Cortex 17:1-8.

Harter MR (1967) Excitability cycles and cortical scanning: a review of two hypotheses of central intermittency in perception. Psychol Bull 68:47-58.

Herrmann CS, Mecklinger A, Pfeifer E (1999) Gamma responses and ERPs in a visual classification task. Clin Neurophysiol 110:636-642.

Herrmann CS, Mecklinger A (2000) Magnetoencephalographic responses to illusory figures: early evoked gamma is affected by processing of stimulus features. Int J Psychophysiol 38:265-281.

Herrmann CS, Bosch V (2001) Gestalt perception modulates early visual processing. Neuroreport 12:901-904.

Herrmann CS, Knight RT (2001) Mechanisms of human attention: Event-related potentials and oscillations. Neurosci Biobehav Rev 25:465-476.

Herrmann CS, Munk MH, Engel AK (2004a) Cognitive functions of gamma-band activity: memory match and utilization. Trends Cogn Sci 8:347-355.

Herrmann CS, Lenz D, Junge S, Busch NA, Maess B (2004b) Memory-matches evoke human gamma-responses. BMC Neurosci 5:13.

Herrmann CS, Senkowski D, Rottger S (2004c) Phase-locking and amplitude modulations of EEG alpha: Two measures reflect different cognitive processes in a working memory task. Exp Psychol 51:311-318.

Herrmann CS, Grigutsch M, Busch NA (2005) EEG oscillations and wavelet analysis. In: Event-related potentials: a methods handbook (Handy TC, ed), pp 229-259. Cambridge: The MIT Press.

Hillyard SA, Kutas M (1983) Electrophysiology of cognitive processing. Annu Rev Psychol 34:33-61.

Horovitz SG, Rossion B, Skudlarski P, Gore JC (2004) Parametric design and correlational analyses help integrating fMRI and electrophysiological data during face processing. Neuroimage 22:1587-1595.

Hughes SW, Crunelli V (2005) Thalamic mechanisms of EEG alpha rhythms and their pathological implications. Neuroscientist 11:357-372.

Isoglu-Alkac U, Basar-Eroglu C, Ademoglu A, Demiralp T, Miener M, Stadler M (2000) Alpha activity decreases during the perception of Necker cube reversals: an application of wavelet transform. Biol Cybern 82:313-320.

Itier RJ, Taylor MJ (2004) Source analysis of the N170 to faces and objects. Neuroreport 15:1261-1265.

Jansen A, Menke R, Sommer J, Forster AF, Bruchmann S, Hempleman J, Weber B, Knecht S (2006) The assessment of hemispheric lateralization in functional MRI--robustness and reproducibility. Neuroimage 33:204-217.

Jansen BH, Brandt ME (1991) The effect of the phase of prestimulus alpha activity on the averaged visual evoked response. Electroencephalogr Clin Neurophysiol 80:241-250.

Jansen BH, Agarwal G, Hegde A, Boutros NN (2003) Phase synchronization of the ongoing EEG and auditory EP generation. Clin Neurophysiol 114:79-85.

Jasiukaitis P, Hakerem G (1988) The effect of prestimulus alpha activity on the P300. Psychophysiology 25:157-165.

Jasper H (1958) Report of committee on methods of clinical exam in EEG. Electroencephalogr Clin Neurophysiol 10:370-375.

Jasper HH, Andrews HL (1938) Electroencephalography III. Normal differentiations of occipital and precentral regions in man. Arch Neurol Psychiatry 39:96-115.

Jausovec N, Jausovec K (2000) Differences in event-related and induced brain oscillations in the theta and alpha frequency bands related to human intelligence. Neurosci Lett 293:191-194.

Jensen O, Tesche CD (2002) Frontal theta activity in humans increases with memory load in a working memory task. Eur J Neurosci 15:1395-1399.

Jensen O, Gelfand J, Kounios J, Lisman JE (2002) Oscillations in the alpha band (9-12 Hz) increase with memory load during retention in a short-term memory task. Cereb Cortex 12:877-882.

Jervis BW, Nichols MJ, Johnson TE, Allen E, Hudson NR (1983) A fundamental investigation of the composition of auditory evoked potentials. IEEE Trans Biomed Eng 30:43-50.

Johnson L, Lubin A, Naitoh P, Nute C, Austin M (1969) Spectral analysis of the EEG of dominant and non-dominant alpha subjects during waking and sleeping. Electroencephalogr Clin Neurophysiol 26:361-370.

Jones SR, Pinto DJ, Kaper TJ, Kopell N (2000) Alpha-frequency rhythms desynchronize over long cortical distances: a modeling study. J Comput Neurosci 9:271-291.

Kalcher J, Pfurtscheller G (1995) Discrimination between phase-locked and non-phase-locked event-related EEG activity. Electroencephalogr Clin Neurophysiol 94:381-384.

Kawabata N (1974) Dynamics of the electroencephalogram during performance of a mental task. Kybernetik 15:237-242.

Keil A, Müller MM, Ray WJ, Gruber T, Elbert T (1999) Human gamma band activity and perception of a gestalt. J Neurosci 19:7152-7161.

Kellaway P (1990) An orderly approach to visual analysis: characteristics of the normal EEG of adults and children. In: Current practice of clinical electroencephalography, 2nd Edition (Daly DD, Pedley TA, eds), pp 139-199. New York: Raven Press.

Kirschfeld K (2005) The physical basis of alpha waves in the electroencephalogram and the origin of the "Berger effect". Biol Cybern 92:177-185.

Klimesch W, Pfurtscheller G, Mohl W, Schimke H (1990) Event-related desynchronization, ERD-mapping and hemispheric differences for words and numbers. Int J Psychophysiol 8:297-308.

Klimesch W (1996) Memory processes, brain oscillations and EEG synchronization. Int J Psychophysiol 24:61-100.

Klimesch W (1997) EEG-alpha rhythms and memory processes. Int J Psychophysiol 26:319-340.

Klimesch W, Doppelmayr M, Russegger H, Pachinger T, Schwaiger J (1998) Induced alpha band power changes in the human EEG and attention. Neurosci Lett 244:73-76.

Klimesch W (1999) EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis. Brain Res Rev 29:169-195.

Klimesch W, Sauseng P, Gerloff C (2003) Enhancing cognitive performance with repetitive transcranial magnetic stimulation at human individual alpha frequency. Eur J Neurosci 17:1129-1133.

Klimesch W, Schabus M, Doppelmayr M, Gruber W, Sauseng P (2004a) Evoked oscillations and early components of event-related potentials: an analysis. Int J Bifurcation & Chaos 14:705-718.

Klimesch W, Schack B, Schabus M, Doppelmayr M, Gruber W, Sauseng P (2004b) Phase-locked alpha and theta oscillations generate the P1-N1 complex and are related to memory performance. Cogn Brain Res 19:302-316.

Klimesch W, Hanslmayr S, Sauseng P, Gruber WR (2006) Distinguishing the evoked response from phase reset: A comment to Mäkinen et al. NeuroImage 29:808-811.

Klimesch W, Sauseng P, Hanslmayr S (2007) EEG alpha oscillations: The inhibition-timing hypothesis. Brain Res Rev 53:63-88.

Koles ZJ, Lind JC, Soong AC (1995) Spatio-temporal decomposition of the EEG: a general approach to the isolation and localization of sources. Electroencephalogr Clin Neurophysiol 95:219-230.

Koles ZJ, Soong AC (1998) EEG source localization: implementing the spatio-temporal decomposition approach. Electroencephalogr Clin Neurophysiol 107:343-352.

Kutas M, McCarthy G, Donchin E (1977) Augmenting mental chronometry: the P300 as a measure of stimulus evaluation time. Science 197:792-795.

Lakatos P, Shah AS, Knuth KH, Ulbert I, Karmos G, Schroeder CE (2005) An oscillatory hierarchy controlling neuronal excitability and stimulus processing in the auditory cortex. J Neurophysiol 94:1904-1911.

Larson CL, Davidson RJ, Abercrombie HC, Ward RT, Schaefer SM, Jackson DC, Holden JE, Perlman SB (1998) Relations between PET-derived measures of thalamic glucose metabolism and EEG alpha power. Psychophysiology 35:162-169.

Lehtela L, Salmelin R, Hari R (1997) Evidence for reactive magnetic 10-Hz rhythm in the human auditory cortex. Neurosci Lett 222:111-114.

Lehtonen JB, Lehtinen I (1972) Alpha rhythm and uniform visual field in man. Electroencephalogr Clin Neurophysiol 32:139-147.

Lindsley DB (1960) Attention, consciousness, sleep and wakefulness. In: American handbook of physiology. Section 1, Neurophysiology (Field J, Magoun HW, Hall VE, eds), pp 1553-1593. Washington D.C.: American Physiological Society.

Long GM, Toppino TC, Mondin GW (1992) Prime time: fatigue and set effects in the perception of reversible figures. Percept Psychophys 52:609-616.

Lopes da Silva FH (1999) Event-related potentials: Methodology and quantification. In: Electroencephalography: Basic principles, clinical applications, and related fields., 4th Edition (Niedermeyer E, Lopes da Silva FH, eds), pp 947-957. Baltimore: Williams & Wilkins.

Luck SJ, Heinze HJ, Mangun GR, Hillyard SA (1990) Visual event-related potentials index focused attention within bilateral stimulus arrays. II. Functional dissociation of P1 and N1 components. Electroencephalogr Clin Neurophysiol 75:528-542.

Makeig S, Inlow M (1993) Lapses in alertness: coherence of fluctuations in performance and EEG spectrum. Electroencephalogr Clin Neurophysiol 86:23-35.

Makeig S, Jung TP (1995) Changes in alertness are a principal component of variance in the EEG spectrum. Neuroreport 7:213-216.

Makeig S, Westerfield M, Jung TP, Enghoff S, Townsend J, Courchesne E, Sejnowski TJ (2002) Dynamic brain sources of visual evoked responses. Science 295:690-694.

Makeig S, Debener S, Onton J, Delorme A (2004) Mining event-related brain dynamics. Trends Cogn Sci 8:204-210.

Mäkinen V, Tiitinen H, May P (2005) Auditory event-related responses are generated independently of ongoing brain activity. Neuroimage 24:961-968.

Maloney KJ, Cape EG, Gotman J, Jones BE (1997) High-frequency gamma electroencephalogram activity in association with sleep-wake states and spontaneous behaviors in the rat. Neuroscience 76:541-555.

Maltseva I, Geissler HG, Basar E (2000) Alpha oscillations as an indicator of dynamic memory operations - anticipation of omitted stimuli. Int J Psychophysiol 36:185-197.

Mazaheri A, Picton TW (2005) EEG spectral dynamics during discrimination of auditory and visual targets. Cogn Brain Res 24:81-96.

Mazaheri A, Jensen O (2006) Posterior alpha activity is not phase-reset by visual stimuli. Proc Natl Acad Sci U S A 103:2948-2952.

McCarthy G, Donchin E (1981) A metric for thought: A comparison of P300 latency and reaction time. Science 211:77-80.

Mecklinger A, Kramer AF, Strayer DL (1992) Event related potentials and EEG components in a semantic memory search task. Psychophysiology 29:104-119.

Michel CM, Kaufman L, Williamson SJ (1994) Duration of EEG and MEG alpha suppression increases with angle in a mental rotation task. J Cogn Neurosci 6:139-150.

Mima T, Oluwatimilehin T, Hiraoka T, Hallett M (2001) Transient interhemispheric neuronal synchrony correlates with object recognition. J Neurosci 21:3942-3948.

Min BK, Busch NA, Debener S, Kranczioch C, Hanslmayr S, Engel AK, Herrmann CS (2007) The best of both worlds: phase-reset of human EEG alpha activity and additive power contribute to ERP generation. Int J Psychophysiol [Epub ahead of print].

Mordkoff JT, Yantis S (1993) Dividing attention between color and shape: evidence of coactivation. Percept Psychophys 53:357-366.

Mulholland T, Evans CR (1965) An unexpected artefact in the human electroencephalogram concerning the alpha rhythm and the orientation of the eyes. Nature 207:36-37.

Mulholland TB, Peper E (1971) Occipital alpha and accommodative vergence, pursuit tracking, and fast eye movements. Psychophysiology 8:556-575.

Müller MM, Junghöfer M, Elbert T, Rochstroh B (1997) Visually induced gamma-band responses to coherent and incoherent motion: a replication study. Neuroreport 8:2575-2579.

Naruse Y, Matani A, Hayakawa T, Fujimaki N (2006) Influence of seamlessness between pre- and poststimulus alpha rhythms on visual evoked potential. Neuroimage 32:1221-1225.

Neuper C, Pfurtscheller G (2001) Event-related dynamics of cortical rhythms: frequency-specific features and functional correlates. Int J Psychophysiol 43:41-58.

Nicolelis MA, Fanselow EE (2002) Thalamocortical [correction of Thalamcortical] optimization of tactile processing according to behavioral state. Nat Neurosci 5:517-523.

Niedermeyer E (1990) Alpha-like rhythmical activity of the temporal lobe. Clin Electroencephalogr 21:210-224.

Niedermeyer E (1991) The "third rhythm": further observations. Clin Electroencephalogr 22:83-96.

Niedermeyer E (1997) Alpha rhythms as physiological and abnormal phenomena. Int J Psychophysiol 26:31-49.

Niedermeyer E (1999) The normal EEG of the waking adult. In: Electroencephalography: Basic principles, clinical applications, and related fields., 4th Edition (Niedermeyer E, Lopes da Silva FH, eds), pp 149-173. Baltimore: Williams & Wilkins.

Nunez PL, Wingeier BM, Silberstein RB (2001) Spatial-temporal structures of human alpha rhythms: theory, microcurrent sources, multiscale measurements, and global binding of local networks. Hum Brain Mapp 13:125-164.

Nunn CM, Osselton JW (1974) The influence of the EEG alpha rhythm on the perception of visual stimuli. Psychophysiology 11:294-303.

Ohla K, Busch NA, Dahlem MA, Herrmann CS (2005) Circles are different: the perception of Glass patterns modulates early event-related potentials. Vision Res 45:2668-2676.

Ota T, Toyoshima R, Yamauchi T (1996) Measurements by biphasic changes of the alpha band amplitude as indicators of arousal level. Int J Psychophysiol 24:25-37.

Palva S, Linkenkaer-Hansen K, Näätänen R, Palva JM (2005) Early neural correlates of conscious somatosensory perception. J Neurosci 25:5248-5258.

Petsche H, Pockberger H, Rappelsberger P (1986) EEG topography and mental performance. In: Topographic mapping of the brain (Duffy FH, ed), pp 63-98. Boston: Butterworths.

Pfefferbaum A, Ford J, Johnson JR (1983) Manipulation of P3 latency: Speed vs. accuracy instructions. Electroencephalogr Clin Neurophysiol 55:188-197.

Pfurtscheller G, Aranibar A (1977) Event-related cortical desynchronization detected by power measurements of scalp EEG. Electroencephalogr Clin Neurophysiol 42:817-826.

Pfurtscheller G (1992) Event-related synchronization (ERS): an electrophysiological correlate of cortical areas at rest. Electroencephalogr Clin Neurophysiol 83:62-69.

Pfurtscheller G, Stancák Jr. A, Neuper C (1996) Event-related synchronization (ERS) in the alpha band - An electrophysiological correlate of cortical idling: A review. Int J Psychophysiol 24:39-46.

Pfurtscheller G, Lopes da Silva FH (1999) Event-related EEG/MEG synchronization and desynchronization: basic principles. Clin Neurophysiol 110:1842-1857.

Pfurtscheller G (2001) Functional brain imaging based on ERD/ERS. Vision Res 41:1257-1260.

Picton TW, Hillyard SA (1988) Endogenous event-related potentials. In: Handbook of Electroencephalography and Clinical Neurophysiology (Picton TW, ed), pp 361-426. Amsterdam: Elsevier.

Polich J, Alexander JE, Bauer LO, Kuperman S, Morzorati S, O'Connor SJ, Porjesz B, Rohrbaugh J, Begleiter H (1997) P300 topography of amplitude/latency correlations. Brain Topogr 9:275-282.

Pollen DA, Trachtenberg MC (1972) Some problems of occipital alpha block in man. Brain Res 41:303-314.

Price GW (1997) The effect of pre-stimulus alpha activity on the auditory P300 paradigm: a prospective study. Brain Topogr 9:169-176.

Pritchard WS (1992) The brain in fractal time: 1/f-like power spectrum scaling of the human electroencephalogram. Int J Neurosci 66:119-129.

Proverbio AM, Zani A (2002) Electromagnetic manifestations of mind and brain. In: The cognitive electrophysiology of mind and brain (Zani A, Proverbio AM, eds), pp 13-40. New York: Academic press.

Rahn E, Basar E (1993a) Enhancement of visual evoked potentials by stimulation during low prestimulus EEG stages. Int J Neurosci 72:123-136.

Rahn E, Basar E (1993b) Prestimulus EEG-activity strongly influences the auditory evoked vertex response: a new method for selective averaging. Int J Neurosci 69:207-220.

Ravden D, Polich J (1998) Habituation of P300 from visual stimuli. Int J Psychophysiol 30:359-365.

Ray WJ, Cole HW (1985) EEG alpha activity reflects attentional demands, and beta activity reflects emotional and cognitive processes. Science 228:750-752.

Rice DM, Hagstrom EC (1989) Some evidence in support of a relationship between human auditory signal-detection performance and the phase of the alpha cycle. Percept Mot Skills 69:451-457.

Salmelin R, Hari R (1994) Spatiotemporal characteristics of sensorimotor neuromagnetic rhythms related to thumb movement. Neuroscience 60:537-550.

Sauseng P, Klimesch W, Doppelmayr M, Pecherstorfer T, Freunberger R, Hanslmayr S (2005a) EEG alpha synchronization and functional coupling during top-down processing in a working memory task. Hum Brain Mapp 26:148-155.

Sauseng P, Klimesch W, Stadler W, Schabus M, Doppelmayr M, Hanslmayr S, Gruber WR, Birbaumer N (2005b) A shift of visual spatial attention is selectively associated with human EEG alpha activity. Eur J Neurosci 22:2917-2926.

Sayers BM, Beagley HA, Henshall WR (1974) The mechanism of auditory evoked EEG responses. Nature 247:481-483.

Schack B, Klimesch W (2002) Frequency characteristics of evoked and oscillatory electroencephalic activity in a human memory scanning task. Neurosci Lett 331:107-110.

Schack B, Weiss S, Rappelsberger P (2003) Cerebral information transfer during word processing: where and when does it occur and how fast is it? Hum Brain Mapp 19:18-36.

Schack B, Klimesch W, Sauseng P (2005) Phase synchronization between theta and upper alpha oscillations in a working memory task. Int J Psychophysiol 57:105-114.

Schroeder CE, Steinschneider M, Javitt DC, Tenke CE, Givre SJ, Mehta AD, Simpson GV, Arezzo JC, Vaughan HG, Jr. (1995) Localization of ERP generators and identification of underlying neural processes. Electroencephalogr Clin Neurophysiol Suppl 44:55-75.

Schürmann M, Basar-Eroglu C, Basar E (1997) A possible role of evoked alpha in primary sensory processing: common properties of cat intracranial recordings and human EEG and MEG. Int J Psychophysiol 26:149-170.

Schürmann M, Demiralp T, Basar E, Basar-Eroglu C (2000) Electroencephalogram alpha (8-15 Hz) responses to visual stimuli in cat cortex, thalamus, and hippocampus: a distributed alpha network? Neurosci Lett 292:175-178.

Sclabassi RJ, Sonmez M, Sun M (2001) EEG source localization: a neural network approach. Neurol Res 23:457-464.

Sewards TV, Sewards MA (1999) Alpha-band oscillations in visual cortex: part of the neural correlate of visual awareness? Int J Psychophysiol 32:35-45.

Shah AS, Bressler SL, Knuth KH, Ding M, Mehta AD, Ulbert I, Schroeder CE (2004) Neural dynamics and the fundamental mechanisms of event-related brain potentials. Cereb Cortex 14:476-483.

Shaw JC (1996) Intention as a component of the alpha-rhythm response to mental activity. Int J Psychophysiol 24:7-23.

Short PL (1953) The objective study of mental imagery. Br J Psychol 44:38-51.

Skrandies W (1984) Scalp potential fields evoked by grating stimuli: effects of spatial frequency and orientation. Electroencephalogr Clin Neurophysiol 58:325-332.

Skrandies W (1998) Evoked potential correlates of semantic meaning--A brain mapping study. Cogn Brain Res 6:173-183.

Smith ME, McEvoy LK, Gevins A (1999) Neurophysiological indices of strategy development and skill acquisition. Cogn Brain Res 7:389-404.

Srinivasan R, Winter WR, Nunez PL (2006) Chapter 3 Source analysis of EEG oscillations using high-resolution EEG and MEG. Prog Brain Res 159:29-42.

Steriade M, Gloor P, Linás RR, Lopes da Silva FH, Mesulam M-M (1990) Basic mechanisms of cerebral rhythmic activities. Electroencephalogr Clin Neurophysiol 76:481-508.

Steriade M, Dossi RC, Nunez A (1991) Network modulation of a slow intrinsic oscillation of cat thalamocortical neurons implicated in sleep delta waves: cortically induced synchronization and brainstem cholinergic suppression. J Neurosci 11:3200-3217.

Steriade M, McCormick DA, Sejnowski TJ (1993) Thalamocortical oscillations in the sleeping and aroused brain. Science 262:679-685.

Steriade M (1999) Cellular substrates of brain rhythms. In: Electroencephalography: Basic principles, clinical applications, and related fields., 4th Edition (Niedermeyer E, Lopes da Silva FH, eds), pp 28-75. Baltimore: Williams & Wilkins.

Strüber D, Basar-Eroglu C, Miener M, Stadler M (2001) EEG gamma-band response during the perception of Necker cube reversals. Visual Cogn 8:609-621.

Strüber D, Herrmann CS (2002) MEG alpha activity decrease reflects destabilization of multistable percepts. Cogn Brain Res 14:370-382.

Suffczynski P, Kalitzin S, Pfurtscheller G, Lopes da Silva FH (2001) Computational model of thalamo-cortical networks: dynamical control of alpha rhythms in relation to focal attention. Int J Psychophysiol 43:25-40.

Surwillo WW (1963) The relation of simple response time to brain-wave frequency and the effects of age. Electroencephalogr Clin Neurophysiol 15:105-114.

Surwillo WW (1964) The Relation of Decision Time to Brain Wave Frequency and to Age. Electroencephalogr Clin Neurophysiol 16:510-514.

Tallon-Baudry C, Bertrand O, Delpuech C, Pernier J (1996) Stimulus specificity of phase-locked and non-phase-locked 40 Hz visual responses in human. J Neurosci 16:4240-4249.

Tallon-Baudry C, Bertrand O, Delpuech C, Permier J (1997) Oscillatory gamma-band (30-70 Hz) activity induced by a visual search task in humans. J Neurosci 17:722-734.

Tallon-Baudry C, Bertrand O (1999) Oscillatory gamma activity in humans and its role in object representation. Trends Cogn Sci 3:151-162.

Tallon-Baudry C, Bertrand O, Fischer C (2001) Oscillatory synchrony between human extrastriate areas during visual short-term memory maintenance. J Neurosci 21:RC177.

Tallon C, Bertrand O, Bouchet P, Pernier J (1995) Gamma-range activity evoked by coherent visual stimuli in humans. Eur J Neurosci 7:1285-1291.

Taylor FM (1981) A case for observing the on-going EEG during averaging of visual evoked potentials. J Electrophysiol Tech 7:216-225

Tiihonen J, Hari R, Kajola M, Karhu J, Ahlfors S, Tissari S (1991) Magnetoencephalographic 10-Hz rhythm from the human auditory cortex. Neurosci Lett 129:303-305.

Tiitinen H, Sinkkonen J, Reinikainen K, Alho K, Lavikainen J, Näätänen R (1993) Selective attention enhances the auditory 40-Hz transient response in humans. Nature 364:59-60.

Trimble JL, Potts AM (1975) Ongoing occipital rhythms and the VER. I. Stimulation at peaks of the alpha-rhythm. Invest Ophthalmol 14:537-546.

Varela FJ, Toro A, John ER, Schwartz EL (1981) Perceptual framing and cortical alpha rhythm. Neuropsychologia 19:675-686.

Verleger R (1997) On the utility of P3 latency as an index of mental chronometry. Psychophysiology 34:131-156.

von Stein A, Chiang C, König P (2000) Top-down processing mediated by interareal synchronization. Proc Natl Acad Sci U S A 97:14748-14753.

Walter VJ, Walter WG (1949) The central effects of rhythmic sensory stimulation. Electroencephalogr Clin Neurophysiol 1:57-86.

Wertheim AH (1974) Oculomotor control and occipital alpha activity: a review and a hypothesis. Acta Psychol (Amst) 38:235-256.

Wertheim AH (1981) Occipital alpha activity as a measure of retinal involvement in oculomotor control. Psychophysiology 18:432-439.

WIKIPEDIA (2007) Mind [online]. [Accessed 15th January 2007]. Available from World Wide Web:<http://en.wikipedia.org/wiki/Mind>.

Yeung N, Bogacz R, Holroyd CB, Cohen JD (2004) Detection of synchronized oscillations in the electroencephalogram: an evaluation of methods. Psychophysiology 41:822-832.

Zani A, Proverbio AM (1995) ERP signs of early selective attention effects to check size. Electroencephalogr Clin Neurophysiol 95:277-292.

Zimbardo PG, Gerrig RJ (2002) Perception. In: Foundations of cognitive psychology: core readings (Levitin DJ, ed), pp 133-188. Cambridge, MA: The MIT Press.

Abstract

Title: The top-down function of prestimulus EEG alpha activity
Author: Byoung Kyong Min, M.Sc. (Neurobiology and Physiology)

Through this thesis, I tried to investigate the functional dynamics of prestimulus alpha activity and its relation to mental events. For this purpose, I categorized subjects according to either the amount or the dominance of prestimulus alpha activity, and employed a transform based on Morlet wavelets for computing total and evoked alpha activity. Study 1 demonstrated the existence of an additive power after stimulation irrespective of the amount of prestimulus alpha activity, while Study 2 provided substantial evidence (dominance-dependency) in favor of phase-resetting of ongoing alpha activity in ERP-generation. Taken together, both models for ERP-generation are evenly plausible within a single framework and able to coexist. Both Study 1 and Study 2 also suggested that prestimulus alpha activity, which presumably reflects a functional state of the brain prior to stimulation, might influence poststimulus information processes. In agreement with this view, Study 3 proposed that prestimulus alpha activity probably reflects top-down inhibitory processing in advance of stimulation and modulates subsequent poststimulus responses. I suppose that a concentrated mental attitude to process upcoming information results in enhancement of alpha activity. Both ongoing top-down reflection and a paradoxical increase of alpha activity can be understandable within this framework.

Zusammenfassung

Title: The top-down function of prestimulus EEG alpha activity
Author: Byoung Kyong Min, M.Sc. (Neurobiologie und Physiologie)

Menschliche EEG Alpha Aktivität im Bereich der parieto-okzipitalen Region ist charakterisiert durch eine erhöhte Amplitude und Dominanz gegenüber anderen Frequenzbändern, sowohl im spontanen EEG als auch in Vorreizabschnitten. Als Folge solch hoher Vorreiz-Alpha-Energie zeigt nur das Alpha Band sowohl ereigniskorrelierte Desynchronisation als auch Synchronisation. Diese besonderen Eigenschaften der Alpha Aktivität bieten geeignete Bedingungen, um die funktionelle Bedeutung der fortlaufenden Aktivität und ihre mutmaßliche Rolle für eine fortlaufende top-down Kontrolle weiterer Informationsverarbeitungsschritte zu untersuchen. Auf der Basis dieser erwähnten Bedingungen habe ich versucht, die folgenden Hypothesen in diesem Dissertationsprojekt zu prüfen. In Studie 1 habe ich die Validität etablierter Modelle, die versuchen, die Entstehung ereigniskorrelierter Potentiale (EKP) zu erklären, mithilfe dissoziierbarer EEG Dynamik von totaler und evozierter Alpha Aktivität geprüft. Als zweites, in Studie 2, habe ich untersucht, ob die Dominanz der Vorreiz-Alpha-Aktivität frühe EKP-Komponenten zugunsten von Phasen-Rückstellungen beeinflusst. Die Ergebnisse dieser Studie validierten darüber hinaus die funktionelle Bedeutung fortlaufender Alpha Aktivität für die Entstehung von EKPs. Schließlich habe ich in Studie 3 die Rolle der Vorreiz-Alpha-Aktivität in Bezug auf eine Form von top-down Kontrolle der Antwort auf einen Reiz untersucht.

Um die Spektralanalyse in dieser Arbeit durchzuführen habe ich die Wavelet Transformation benutzt. Zur Detektion sinusoidaler EEG Signale sind sinusoidale Wavelets, wie etwa Morlet Wavelets, ideal. Deshalb habe ich eine Transformation auf der Basis von Morlet Wavelets benutzt, um totale und evozierte Alpha Aktivität zu berechnen. Die totale Aktivität besteht aus evozierter und induzierter Aktivität. Evozierte Aktivität ist streng phasengebunden zum Beginn eines Ereignisses über die Versuchsdurchgänge hinweg, während induzierte Aktivität zwar mit den Experimentalbedingenen korreliert, jedoch keine fixe Phasenrelation zum Beginn eines Ereignisses zeigt.

In Untersuchung 1 (Kapitel 4) wurde die Beziehung zwischen Vorreizausprägung fortlaufender Alpha Aktivität und seiner ereignisskorrelierten Dynamik mit Bezug auf Modelle der EKP Entstehung untersucht. Es gibt verschiedene konkurrierende Hypothesen über die Genese der EKP. Während einige Autoren vorgeschlagen haben, dass EKP durch

eine neuronale Antwort generiert würden, die sich zur fortlaufenden Aktivität additiv und unabhängig verhält, haben andere argumentiert, dass EKPs durch eine teilweise Phasenrückstellung der fortlaufenden Aktivität entstünden. Um die Gültigkeit dieser zwei Modelle abzuschätzen, wurde das EEG bei 23 Versuchspersonen während einer visuellen Diskriminationsaufgabe gemessen. Nachdem die Versuchspersonen auf der Basis der Stärke ihrer totalen Vorreiz-Alpha-Aktivität einer von drei Gruppen zugeordnet wurden, konnten ausgeprägte Unterschiede der ereigniskorrelierten EEG Dynamik zwischen den Gruppen beobachtet werden. Obwohl alle Gruppen eine ereignisskorrelierte Zunahme der phasengebundenen (evozierten) Alpha Aktivität zeigten, zeigten nur Versuchspersonen mit anhaltender Vorreiz-Alpha-Aktivität eine deutliche Abnahme nicht phasenstarrer Alpha Aktivität nach dem Reiz (Alpha-Blockade). Im Gegensatz dazu zeigten Versuchspersonen ohne beobachtbare totale Vorreizaktivität eine gleichzeitige Zunahme von phasengebundener und nicht phasengebundener Alpha Aktivität nach der Stimulation. Die Daten dieser Versuchspersonen schienen für eine additive neuronale Antwort ohne Alpha-Blockade zu sprechen. Allerdings legen die dissoziierbaren EEG Dynamiken von totaler und evozierter Alpha Aktivität sowie eine komplementäre Simulation eine teilweise nicht-lineare Komponente der EKP Entstehung nahe. Wir schlußfolgerten, dass sowohl teilweise Phasenrücksetzung, als auch teilweise additive Energiezunahme dynamisch zur Genese der EKPs beitragen. Diese Ergebnisse zeigen, dass der Vorreizzustand des Gehirnes einen deutlichen Einfluß auf ereignisskorrelierte Hirnantworten ausübert, und dass sich die Mechanismen, die ereignisskorrelierte Antworten erzeugen, je nach Vorreizzustand unterscheiden können. Diese Studie wurde im *International Journal of Psychophysiology* veröffentlicht.

Um genauer zu untersuchen, ob eine Reorganisation der fortlaufenden Alpha Aktivität in Studie 1 nach der Stimulation auftrat, wurde in Studie 2 (Kapitel 5) der Zusammenhang zwischen der Dominanz der totalen Vorreiz-Alpha-Aktivität und nachfolgenden evozierten Antworten untersucht. Dazu wurden die Versuchspersonen erneut auf zwei Untergruppen verteilt: dominantes und nicht-dominantes Alpha, je nach der Dominanz der totalen Vorreiz-Alpha-Aktivität im gleichen Datensatz wie in Studie 1. Es konnte beobachtet werden, dass Individuen mit dominanter Vorreiz-Alpha-Aktivität deutlich höhere Amplituden der P1 erzeugen, als solche ohne dominante Vorreiz-Alpha-Aktivität. Solch eine proportionale Beziehung zwischen Vorreiz-Alpha-Dominanz und der P1-Amplitude kann kaum durch die Modellvorstellung einer additiven Energiekomponente erklärt werden, in der die Stimulation systematisch evozierte Signalenergie – unabhängig von den Eigenschaften der Vorreiz- und fortlaufenden Aktivität – zur fortlaufenden Aktivität hinzu addiert. Eher scheint die Dominanz der

Vorreiz-Alpha-Aktivität mit einem Beitrag der Nachreiz-Alpha-Aktivität zu solch einer frühen EKP Komponente wie der P1 einherzugehen, zu Gunsten einer Phasenrückstellung der fortlaufenden Alpha-Aktivität. Da die frühen EKPs reizinduzierte, unverzügliche Hirnantworten widerspiegeln, unterstützen diese Befunde auch die Auffassung, dass die dominante Vorreiz-Alpha-Aktivität einen bestimmten Zweck in Hinsicht auf mentale Prozesse hat. Die Dominanz von Vorreiz-Alpha-Aktivität, die vermutlich einen funktionalen Zustand des Gehirns vor der Stimulation widerspiegelt, kann die Informationsverarbeitung, wie sie sich in frühen EKP Komponenten widerspiegelt, möglicherweise durch Phasenrückstellung beeinflussen. Diese Studie ist zur Zeit unter Begutachtung bei der Zeitschrift *Clinical Neurophysiology.*

In Studie 3 (Kapitel 6) wurde die Funktion der Vorreiz-Alpha-Aktivität in Bezug zu Vorreiz top-down Hemmungsprozessen untersucht. Um diese Hypothese zu testen, wurde das EEG von 16 Versuchspersonen während einer Farb- und einer Form-Diskriminationsaufgabe aufgezeichnet. Beide Aufgaben erforderten die Unterdrückung der aufgabenirrelevanten Reizdimension. Längere Reaktionszeiten und P3 Latenzen zeigten, dass die Formaufgabe schwieriger als die Farbaufgabe war. Es wurde angenommen, dass diese verschiedenen Aufgabenschwierigkeiten durch die höhere Salienz der Farbeigenschaft im Vergleich zur Formeigenschaft bedingt waren. Interessanterweise wurde deutlich mehr totale Vorreiz-Alpha-Aktivität während der Formaufgabe als in der Farbaufgabe beobachtet. Es kann geschlossen werden, dass die Unterdrückung der salienteren Farbeigenschaft während der Formaufgabe eine erhöhte Vorreiz-Alpha-Aktivität zur Folge hatte. Solche Reflektionen der Leistung nach dem Reiz in der Alpha-Aktivität vor dem Reiz legen nahe, dass die Vorreiz-Alpha-Aktivität top-down-Prozesse zur Vorbereitung der nachfolgenden Aufgaben-Leistung widerspiegelt. Da dieser Aufgabeneffekt der Vorreiz-Alpha-Aktivität sowohl bezüglich der Reaktionszeiten als auch bezüglich der P3 Latenzen beobachtet wurde, scheint die Vorreiz-Alpha-Aktivität solche, dem Reiz folgende, Antworten vorherzusagen. Diese Studie ist im Druck bei der Zeitschrift *Neuroscience Letters*.

Zusammenfassend kann man sagen, dass fortlaufende EEG Aktivität durch eine Mischung von additiver Signalenergie und der Neuordnung der Vorreiz-Aktivität erregt werden. Diese Phänomene wurden im vorliegenden Projekt, zumindest für das EEG Alpha Band, beobachtet. Sowohl Studie 1 als auch Studie 2 legen nahe, dass Vorreiz-Alpha-Aktivität, die wahrscheinlich den funktionellen Zustand des Gehirns vor einer Stimulation widerspiegelt, dem Reiz folgende Informationsverarbeitungsprozesse beeinflussen kann.

Studie 3 lieferte eine tatsächliche Evidenz für einen funktionellen Zusammenhang zwischen Vorreiz-Alpha-Aktivität und top-down Verarbeitung. Ich vermute, dass eine konzentrierte mentale Anstrengung anstehende Information zu verarbeiten, zu einer Verstärkung der Alpha-Aktivität führt. Daraus schließe ich, dass eine dominante Vorreiz-Alpha-Aktivität möglicherweise fortlaufende top-down Informationen widerspiegelt und nachfolgende Reizantworten moduliert.

Declaration (Erklärung)

Hiermit erkläre ich, daß ich die von mir eingereichte Dissertation zum dem Thema "The top-down function of prestimulus EEG alpha activity" selbständig verfaßt, nicht schon als Dissertation verwendet habe und die benutzten Hilfsmittel und Quellen vollständig angegeben wurden.

Weiterhin erkläre ich, daß ich weder diese noch eine andere Arbeit zur Erlangung des akademischen Grades doctor rerum naturalium (Dr. rer. nat.) an anderen Einrichtungen eingereicht habe.

Magdeburg / 3 Juli 2007	*Byoung Kyong Min*
Ort / Datum	Unterschrift

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- As Matter Makes Mind, Mind Makes Matter -

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Magdeburg / 3 Juli 2007	*Byoung Kyong Min*
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Publications

Journal articles

Min BK, Busch NA, Debener S, Kranczioch C, Hanslmayr S, Engel AK, Herrmann CH, 'The best of both worlds: phase-reset of human EEG alpha activity and additive power contribute to ERP generation' *International Journal of Psychophysiology*, [Epub ahead of print], 2007

Min BK, Herrmann CH, 'Prestimulus EEG alpha activity reflects prestimulus top-down processing' *Neuroscience Letters*, in press

Choi JM, Bae BH, **Min BK**, Kim SY, 'The analysis of brain activity in wakefulness and deep sleep states from a dog EEG' *Journal of the Korean Physical Society*, Vol. 30, No. 2, April 1997, pp. 328-33

Book chapter and Booklet

Herrmann CS, Pauen M, **Min BK**, Busch NA, Rieger J, 'Eine neue interpretation von Libets experimenten aus der analyse einer wahlreaktionsaufgabe' In Herrmann CS, Pauen M, Rieger J, Schicktanz S (ed.), "*Bewusstsein (Consciousness)*", pp. 120-134, Utb. 2005 (ISBN 3-8252-2686-7)

Min BK, 'MIND' (Neuroscience E-book in Korean PDF version), Mind21, 2000 (ISBN 89-89350-00-X)

Abstracts and Conference proceedings

Min BK, Busch NA, Debener S, Engel AK, Herrmann CH, 'Evoked Visual Alpha activity reflects Cognitive processing' The 11th Annual Meeting of *Cognitive Neuroscience Society*, San Francisco, USA, April 2004; Printed in 'Cognitive Neuroscience Society Annual Meeting Program 2004' (A supplement of the *Journal of Cognitive Neuroscience*) p. 81 (B141)

Min BK, Busch NA, Debener S, Engel AK, Herrmann CH, 'Differentiating Evoked and Induced Visual Alpha activity by Exogenous parameters' The 14th *Evoked Potentials*

International Conference (EPIC XIV), University of Leipzig, Germany, March 2004; Printed in 'Evoked Potentials International Conference XIV: Leipzig Series in Cognitive Sciences 5' (A. Widmann et al., eds) p. 110 *Leipziger Universitätsverlag*

Min BK, Kim MS, Youn T, Kim JJ, Kwon JS, 'Event-Related Potentials of a Linguistic Binding Process in a Korean Monosyllabic Word' The 32nd Annual Meeting of *Society for Neuroscience*, Orlando, USA, November 2002; Published at online *2002 Abstract Viewer/Itinerary Planner.* Program No. 279.7. Washington, DC: Society for Neuroscience

Min BK, Kim MS, Youn T, Kim JJ, Kwon JS, 'Event-Related Potentials of a Monosyllabic Word' The 16th Annual Conference of *The Korean Society for Cognitive Science*, Busan, Korea, May 2002

Min BK, Park HJ, Kang DH, Youn T, Kim MS, Kwon JS, 'Time-frequency analysis of 40Hz in oddball paradigm in schizophrenia: Preliminary study' Annual conference of *Korean Neuropsychiatric Association*, Seoul, Korea, October 2001

Miscellaneous

Min BK, 'Light-induced Synchronization of the Suprachiasmatic Neural Network: Converting Glutamate to GABA' (*Northwestern University* (USA), The Graduate School, Department of Neurobiology and Physiology, M.S. Thesis: June 19, 1998)

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Academic Affiliations

2003-present	Association for the Scientific Study of Consciousness
2002-present	Korean Brain Society
2002-present	Society for Neuroscience
2001-present	Cognitive Neuroscience Society
2001-present	Korean Society for Cognitive Science
1996-present	American Association for the Advancement of Science

Honors, Scholarships and Fellowships

2002 Jul	DAAD-KOSEF Scholarship (Summer Institute Program) DAAD (Deutscher Akademischer Austausch Dienst) and KOSEF (Korea Science and Engineering Foundation) Joint-Program
2000 Dec	Award at the Korea Digital Contents Contest, SoftExpo 2000 Ministry of Information and Communication, Korea
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Other Professional Experiences and Activities

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2000-2001	Contribution of Neuroscience essays to Korea Science Foundation official webzine

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