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COGNITIVE ELECTROPHYSIOLOGY AND ATTENTION

Early evoked EEG components, attention and brain oscillations

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Contents

Attention is one of the most popular constructs in modern cognitive psychology, psychophysiology and related fields. After more than 100 years of investigation the study of its psychological and neural mechanisms continues and still generates intense controversy (e.g., Allport, 1993; Näätänen, 1992). The concept of attention seems to be essential for us humans as perceiving, thinking and behaving organisms. The aim of the first section is to review some of the research on attention and to provide some background on which "early evoked EEG components (P1, N1, P2) and brain oscillations" – discussed later – can be better understood. Subsequent sections then discuss basics of the electroencephalogram, the event-related potentials (ERPs) and some interesting and crucial work on brain oscillations by Basar et al. (1992, 1996, 1997, 1998) and Klimesch et al. (1996, 1997, 1998, 1999, 2000, 2001) discussing especially EEG alpha and theta oscillations. Finally I will try to "bridge the gap" between the latter two approaches at first by elaborating on a working model and subsequently by presenting some experimental - and I hope intimidating - evidence suggesting a close link between event-related potentials (ERPs) and brain oscillations (predominately in the theta and alpha range). I will finish up by applying the approach used there to some classical visual attention studies using ERPs and argue for further support regarding our hypotheses.

1 <u>Basics of Attention</u>

The very essence of attention and consciousness seems "to reside in shifting processes and states within the central nervous system, some of which are detectable through changes in electrical potentials recorded indirectly and diffusely from the brain, or directly and focally in certain regions of the brain" (Lindsley, 1960, pp. 1554-1555)[1].

Attention "guides" us in scanning or focusing on different objects depending on our momentary or permanent interests and goals as well as on the properties of the stimuli involved.

Besides active or voluntary attention, where we can choose the object of our attention there are also other significant or distracting stimuli (e.g., abrupt loud sounds, unfamiliar objects or events, or our name) that tend to attract our attention away from the task we are performing. William James (1890)[1] named this attention switch "passive attention"; stimuli that elicit passive attention also tend to elicit what is called the "orienting response" (Sokolov, 1963)[1]. "Here we are facing a biologically vital mechanism which forcefully provides us environmental information when its potential significance is at its highest (onset, offset, change, regularity in irregularity or noise)" (Näätänen, 1992, p. 71).

In perceptually static situations when our mental activity momentarily has no definite goal, associative chains of thoughts are postulated; that is one thought activating the next or one memory calling for another. Usually our thinking however has a goal and can thus be characterized as directed thinking or "mental work" (Roland, 1985)[1]. The thinking process is steadily self-corrected until the desired end goal is achieved (Ingvar, 1985)[1].

It is interesting to note that attention is heavily dependent upon timing, that is if timing is not adjusted to a stimulus, the stimulus is not going to be perceived or recognized. It seems as if attention has the ability to increase the probability for excitatory events, whereas in addition inhibition afore is needed to enhance the "signal-to-noise ratio".

The ability to concentrate on the activity pursued or the ability to maintain mental focus and to shift it according to the changing environment is crucial for any human being and most likely, for any living creature.

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[1] Cited in Näätänen (1992)

2   <u>Electroencephalography (EEG): Basic Principles</u>

Permanent environmental stimuli trigger sequences of physiological processes, which then provide us with the required responses. Those psychophysiological processes are a potential source for understanding the information processing that takes place between stimulus and response.

Many psychophysiological research methods are clarifying cerebral mechanisms of attentive and automatic information processing quite indirectly, like the classical GSR (galvanic skin response), which is a measurement of the skin-conductance response. Since 1875 as Caton first managed to conduct the "feeble currents of the mind" methods like the use of the electroencephalogram (EEG) enable us to perform direct studies of the cortical activity and help to evaluate the cognitive physiological processes. With event related potential (ERP) studies, for example, we are "quite close'' to the ultimate objects of interest, with "only" skull, scalp, and dura mater separating us from the target process or mechanism.

The EEG records the electrical activity of many hundreds of thousands cortical neurons through electrodes placed on the scalp and is a helpful device to examine these collective or ensemble properties characteristic of the cerebral cortex. The electroencephalogram is based on the theory of volume conduction, which describes the flow of ionic current generated by nerve cells through the extracellular space. Potential changes recorded from the scalp are generated by the summed ionic currents of the many thousands of neurons, more so from the cortex then subcortical areas, located under the recording electrode.

Surface recorded scalp potentials reflect mainly the activity of cortical neurons in the area underlying the EEG electrode, one estimate suggests that $6 \ cm^2$ of cortical surface area must be synchronously activated for a cortical potential to be detected (Karl, 1993, cited in Näätänen, 1992). Furthermore EEG recordings reflect postsynaptic rather than action potentials, for two reasons. First, postsynaptic potentials extend over a larger portion of the membrane, and thus generate a field that corresponds rather to a dipole perpendicular to the membrane surface. Secondly, action potentials, owing to their short duration (1-2 msec), tend to overlap much less than do postsynaptic potentials (EPSP and IPSP), which last substantially longer (approx. 10-250 msec) (Lopes da Silva & Van Rotterdam, 1999). The electrical activity of pyramidal cells is the principal source of EEG potentials, because the apical dendrites of those cells are parallel to one another and always oriented perpendicular to the brain surface, further they often cross several layers and thus allow input from different cortical layers to be integrated along the dendritic tree.

The recording electrodes are usually placed over the frontal, parietal, occipital and temporal lobes according to conventional schemes e.g., the International 10-20 system with 19 electrode sites (Jasper, 1958) or modified and extended arrangements (e.g., that of the American EEG Society, 1994, specifying 75 electrode positions).

The EEG technique provides not only an important source for studying certain normal behavioral states, such as sleep, dreaming, wakefulness, and arousal, but has also significant clinical applications, e.g. for diagnosing certain disease states, such as epilepsy and coma.

EEG can be recorded either while the participant is remaining calm or sleeping, or during specific sensory stimulation, such as presentation of tones or visual stimuli. The EEG components related specifically to a significant stimulus are referred to as sensory evoked potentials and event-related potentials (ERP). Sensory evoked potentials reflect the processing of the physical characteristic of a stimulus and are therefore clinically useful in assessing the function of sensory systems or evaluating demyelinating diseases. These potentials consist of multiple components because they reflect cortical processing as well as early subcortical processing. These first set of deflections are called brain stem evoked potentials and are sometimes also referred to as far-field potentials because they originate from distant subcortical sites. Event-related potentials on the other hand are (defined to be) dependent upon the context in which the stimulus is presented, such as whether the stimulus is expected or a surprise.

2.1   Spontaneous frequencies of the brain (EEG - rhythms)

The frequencies of the potentials recorded from the scalp of normal humans typically vary from 0.5-50 Hz, and the amplitudes typically lie between 10 and 100μV (in adults, more commonly between 10 and 50μV) (Basar, 1998; Niedermeyer, 1999).
The four dominant frequency bands typically observed are called alpha (8-13 Hz), beta (13-30 Hz), delta (0.5-4 Hz) and theta (4-7 Hz). The sequence of these Greek letters is not logical and can only be understood in historical terms.

Since even the earliest empirical findings in EEG research the alpha rhythm presents itself as the most dominant brain oscillations in the human EEG and was the first to be observed by Berger. The alpha rhythm does tend to increase in amplitude during rest and relaxation and is relatively absent during intellectual functioning. Thus, a strong alpha rhythm can generally be observed in relaxed individuals who are awake with their eyes closed; whereas sensory stimulation or strain during the recording usually causes significant reduction of the alpha rhythm and its replacement with lower voltage, faster frequencies. This finding that alpha

desynchronizes or becomes suppressed during mental activity was already described in the late 1920s by Berger.

The **alpha** (α) rhythm (8-13 Hz) often has a mean frequency centering around 10 Hz in adults - somewhat slower in children - with the maximum voltage over the parietal and occipital electrodes. The amplitude of the posterior alpha rhythm is 15 to 50µV in young adults and is usually higher in the non-dominant hemisphere. However evidence provided by Klimesch (1996, 1999) indicates that within the 8 – 13 Hz alpha range different frequency bands should be distinguished. In a series of experiments Klimesch et al. (e.g., 1996, 1997, 1998) were able to show that desynchronization in the range of about 6.5 – 10.5 Hz (lower alpha) reflects attentional processes whereas upper alpha desynchronization – in the range of about 10.5–12.5 Hz – is selectively associated with processing of sensory-semantic information.

Lopes da Silva (e.g., 1999) or Klimesch (e.g., 1999) for example, note that thalamocortical feedback loops (see Steriade, 1999 for review) play a significant role in generating the alpha-rhythm.

Beta waves (18–30 Hz) occur in all individuals, are usually of low amplitude and are normally distributed maximally over frontal and central regions.

Delta (δ) activity (0.5-4 Hz) is not normally recorded in the awake adult but is a prominent feature of sleep and becomes increasingly dominant during the progress from stage 2 to stage 4 sleep. Delta waves have the largest amplitudes, normally between 20-200µV.

Electroencephalographic activity between 4 and 7 Hz – **theta (θ)** activity - is seen in normal drowsiness and sleep, and during wakefulness in young children. Theta is also present in normal waking adults.

Researchers (e.g., for review see Crawford, 1994) also note that lower theta is associated with drowsiness and higher theta activity with cognitive effort. Some investigators have also postulated that recent memories are consolidated and integrated with existing memories during REM, in which especially hippocampal theta seems to play an essential role. Klimesch (1999) suggested that the encoding of new information might be reflected by theta oscillations in hippocampocortical feedback loops in the awake or more recently (personal communication, June 2001) emphasized the close link of theta to the working memory system (WMS).

The slow brain oscillations – delta and theta activity– in the EEG are also commonly interpreted as an indicator of cortical inhibition.

3   Event-Related Potentials

3.1   An Introduction

Quantitative EEG analyses are traditionally categorized into analyses in the time and the frequency domain (Lopes da Silva, 1999). Event related potentials (ERPs), calculated by additive averaging, are most prominent and well-known example of analyses in the time domain. In the frequency domain a variety of different measures are used which will be briefly discussed later.

Event-related potentials (ERPs) are stimulus-evoked brain responses - voltage changes - recorded from the human scalp that are time-locked to a sensory, motor, or cognitive process, and therefore provide electrophysiological insight onto brain functions during cognition.

By repeating a stimulus several times, and averaging those epochs, background activity not time-locked to the presentation of the stimulus cancels itself out, revealing the underlying event-related cognitive response. These event-related response configurations reflect both the physical parameters of the eliciting stimulus, as well as the perceptual-cognitive processes, which it engages.

For the sake of classification, it has also proved useful to distinguish between exogenous and endogenous components. Components whose characteristic (amplitude, latency, and distribution) seem to depend on physical properties of sensory stimuli, such as their modality and intensity are called "exogenous" or "sensory" components (sometimes also referred to as "evoked potential" or EP) . On the other hand there is another set of components whose characteristics depends on the nature of the subject's interaction with the stimulus, that is they vary as a function of attention, task relevance, and the nature of the processing required for the stimulus. Some can be elicited even when an external event is absent, as for example, when an expected stimulus is omitted. These are the "cognitive" or "endogenous components" (Rugg & Coles, 1995). Generally spoken the ERP components that occur within the first 100 msec after stimulus presentation tend to be more exogenous, while those occurring later tend to be more endogenous (see fig. 1). Note that the endogenous ERP components starting at about 100ms after stimulus are usually not referred to as "early ERP components", but even as the "late components". However, in terms of the "cognitive" (endogenous) components discussed throughout this paper (P1, N1, P2) the notation "early ERP components" for P1, N1 and P2 should be intelligible.
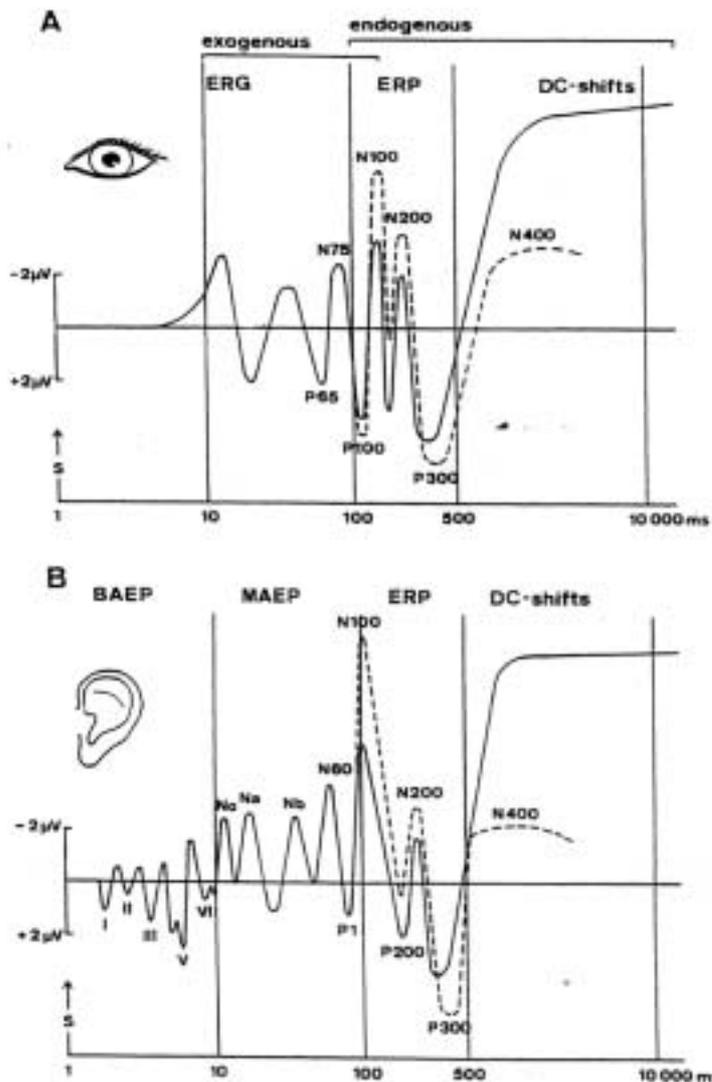
Figure 1. Average event-related responses to visual (A) and acoustic (B) stimuli

Exogenous components comprise the P 65 and N 75 in the visual modality and the acoustic brain stem evoked potentials (BAEP), as well as the mid-latency components (MAEO) in the acoustic modality. Components with latencies longer than 100 ms are considered endogenous in the visual and the acoustic modality, with the latter having a tendency towards shorter latencies. The P100 and N100 components can be modified by orienting and selective attention (dashed lines), the N200 by stimulus evaluation and the P300 by context updating, whereas the N400 is related to semantic expectancy. Exogenous event-related potentials exhibit modality-specific potential-traces, endogenous components on the other hand, are very similar in both modalities (from: Altenmüller & Gerloff, 1999).

It is clear that ERPs provide only a view of those cerebral events that are sufficiently synchronized and organized. "A good deal of cerebral activity occurs without generating electrical activity recordable at the scalp" (Näätänen, 1992, p.79). What is recorded is usually a composite of temporally overlapping effects from multiple cerebral processes.

Although, neuroscientists begin to disentangle different components –if they are differentially sensitive in amplitude or latency to different experimental manipulations – there remains the major concern referred to as the "inverse problem". "This is because the potential

fields of different sources in a volume-conducting space - such as that inside the skull - sum linearly with each other (see Helmholtz's principle of superposition) to give a scalp-recorded potential field which could be produced by any number of source configurations" (Näätänen, 1992, p.81).

3.2 <u>Mechanisms and Models of Selective Attention</u>

"At the most basic level, selective attention can be characterized as the 'filtering' of sensory information, a process that is central to normal human function in that it allows us to rapidly isolate important input from the sensory environment for the highest levels of cognitive analysis" (Handy et al., 2001, p.75). It is well known that events in the external and internal world must compete for control of perception, memory and behavior. As a consequence our perception and awareness of the whole world around us is influenced or even heavily dependent upon these (early) selection processes. These mechanisms underlying the aspects of human conscious experience remain to be completely identified, although much about them is already elucidated. In recent years there have been significant advances in understanding the neural systems that mediate these attentional processes (e.g., Näätänen, 1992; Posner, 1995; Hillyard, Mangun, Woldorff, & Luck, 1995).

It is long known that some components of cerebral evoked potentials may be significantly altered in their appearance by processes of attention and arousal. However a long debated question regarding selective attention concerns the stage of sensory processing at which incoming signals are first selected or rejected by attentional mechanisms. The two main postulates that evolved where the concepts of early (e.g., Broadbent, 1970; Treisman, 1969, cited in Rugg & Coles, 1995) and late (e.g., Deutsch & Deutsch, 1936; Norman, 1968, cited in Rugg & Coles, 1995) selection as possible mechanisms of attentional control over incoming information. Late selection theorists have argued that both attended and irrelevant stimuli are fully analyzed before any selection takes place. Early selection on the other hand suggests that the processing of a stimulus needs not to be completed before the event can either be selected for further processing or rejected as irrelevant.

Another related question is whether attention acts via changes in the sensitivity of the perceptual system or only affects the decision or response applied to attended and unattended events. One should note that the late P300 is widely considered to reflect the final decision and identification processes related to the detection of task-relevant stimuli.

Posner (e.g., 1995) showed that when a prior cue correctly indicated the location of the subsequent target stimulus the reaction times were faster than when the cue indicated an

incorrect target location. Posner suggested that a facilitation of sensory/perceptual processing might underlie the speeded reaction times.

Other signal detection methods also supported the idea that precueing – and thus selective attention - does indeed result in perceptual sensitivity changes, thereby supporting the notion that attention can act at a very early, perceptual level of information processing (e.g., Downing, 1988; Hawkins et al., 1990, cited in Rugg & Coles, 1995).

However, these approaches are not able to specify the neural mechanisms that give rise to the increased sensitivity. Applying psychophysiological methods may help to identify these intermediate neural events that contribute to the ultimate behavioral output. In terms of attentional control, a general distinction is further made between stimulus-driven or bottom-up effects on attentional selection and goal-driven or top-down influences.

In humans, event-related potentials (ERPs) are becoming increasingly useful for the study of selective attention and perception as they can yield information about the timing, sequential order, and anatomical location of e.g. attentional selection processes (Mangun, Hillyard, & Luck, 1993). ERPs are well suited for studying attention because they can provide a more detailed picture of processing at various levels of the nervous system than can be obtained from behavioral methods. (Some already identified and characterized neural generators of specific ERP components will be discussed later on.) ERPs, for example, have been proved useful in investigating how early in the afferent visuocortical pathway spatial attention can modulate stimulus processing.

Another very important advantage of ERP recordings for the study of attention is the fact that they provide a measure of the processing of the stimulus in the absence of any requirement that the subject attends and/or responds to that stimulus. Finally, the high temporal resolution – in the range of milliseconds – of the ERP provides important information about the absolute and relative timing of neural/cognitive events that would be almost impossible to infer from behavior; and that is not available in other physiological methods such as positron emission tomography (PET) or functional magnetic resonance imaging (fMRI).

Consequently some evidence will be presented, demonstrating that early evoked EEG components (i.e., the "P1-N1 complex") reflect sensory and early attentional processes. It is important to note that the reason for focusing on those early ERPs components, as well as (selective) attention lies in their close functional resemblance to the EEG alpha rhythm, discussed later. It's noteworthy, that those early components seem to have a frequency

characteristic that corresponds to an oscillation in the alpha frequency range (somewhere between 6 and 12 Hz).

3.3 <u>Auditory Selective Attention and Feature Selection</u>

In addition to the studies about visual ERPs - reviewed below - there has also been extensive research on ERP indices of selective attention in both auditory and somatosensory modalities. A basic question is whether the principles derived from studies in the visual modality also apply in other sensory systems.

The earliest studies on auditory selective attention focused on the "cocktail party effect" and tried to explain how a human listener can attend to a single conversation in a distracting, noisy environment. For example Cherry (1953, cited in Rugg & Coles, 1995) used dichotic listening tasks to examine the ability of a listener to select a relevant message in one ear while ignoring irrelevant information presented in the other ear. Cherry noted significant performance decrements when the subjects attempted to attend to both input channels (with different stimuli) simultaneously and therefore inferred that attentional resources must be limited.

Related studies showed, that even unattended input channel were constantly monitored, to such an extent that high-priority information - like ones name - could break through the attentional barrier.

Several dichotic listening studies of this type have found that attention affects very early stages of auditory processing; auditory ERP studies by Woldorff and Hillyard (1991) for example indicate that already 20-50 ms post-stimulus the neural processing can differ significantly between attended versus unattended ear information. This attention effect results in a greater positive–polarity voltage deflection in the ERP waveform to attended ear stimuli in the very short latency range of 20-50 ms. Because of this extremely short latency the "P20-50 effect" was interpreted as evidence in favor of the early selection model (of auditory signals). "Using combined ERP and MEG recording, Woldorff et al. (1993) were able to provide strong evidence that the P20-P50 attention effect was generated in the auditory cortex, perhaps as early as the primary sensory receiving area." (Mangun & Hillyard, 1995, p. 67).

Although the P20-50 attention effect seems to be generated in the first stages of auditory cortical processing, it is still possible that these effects reflect stimulus selection that is passed along from earlier, subcortical processing stages. There have been indeed reports of

attentional modulations of very early brainstem-evoked components of the auditory ERPs, but their reliability may be questionable.

It is interesting to note that – in theory - the in the auditory system given efferent neural projections from the olivocochlear bundle to the cochlea, would be potentially able to modulate processing as early as the auditory receptors themselves! But until today no corresponding efferent projections have been demonstrated in the human visual system between the thalamus or other subcortical structures and the retina. Though there is evidence that the majority of synaptic connections onto neurons in the primary visual cortex come from higher order processing areas rather than directly from sensory receptors (e.g., Federmeier & Kutas, 2001).

If we think a moment about the different properties of our visual and auditory system this fact could be compelling. When two different frequencies of sound waves are mixed, we do not perceive an intermediate tone instead we hear both original frequencies, thus our ear is working as an analytical organ. The human eye on the other hand is a synthetic organ; thus we perceive a single color when two different wavelengths of light are mixed. Could it be that this difference relates to the lacking efferent projections in the human visual system? Is the modulation of processing as early as at the receptors themselves perhaps necessary to "split up" a mixed stimulus, so that it can be perceived in (all) its original components?

In comparison to the recently discovered P20-50 effects attentional modulations of longer-latency ERPs were reported already over 20 years ago. Numerous studies predominately have described attention effects on the sensory-evoked N1 component (80-100 ms latency) of the auditory ERP (e.g., Woldorff & Hillyard, 1991). The mechanism suggested to account for the N1 attention effect was a selective filtering of auditory inputs that produced amplitude modulations of the brain generators of the N1 component.

In essence the same mechanism as will be proposed subsequently for the visual P1 and N1 components; The idea being that the neural generators of these sensory-evoked potentials are influenced by descending neural systems in a selective fashion such that those neurons that encode the properties of the attended stimulus are relatively facilitated in comparison to those that encode the features of the unattended stimuli. Hence, it would be reasonable to propose that neural activity reflected by the P20-50 and the N1 form a serial, hierarchical network for cortical auditory information processing.

The N1 attention effect is usually accompanied by a more prolonged negative deflection in the auditory ERP to attended stimuli. Because this longer-lasting negativity can be best

observed by subtracting the ERP to the unattended from the ERP when attended, it was referred to as the "negative difference wave" (Nd).

Näätänen (1992) considered the Nd to be a consequence of an enlarged endogenous component termed the "processing negativity" (PN) elicited by attended-channel stimuli. Näätänen proposed that the PN wave represented the activity of neurons specifically engaged in processing the attended stimuli, which were separate from those neurons that generated the sensory-evoked N1-peak.

Woldorff and Hillyard (1991) concluded that a clear distinction should be made between the N1 attention effect, the P2 attention effect, and a longer-latency negativity (late Nd or PN). But the question remains unresolved whether the early Nd attention effect reflects a modulation of an evoked sensory response (the N1). However, the well established finding of the attentional modulation of the P20-50 evoked activity (e.g., Woldorff et al., 1993) strongly suggest early selection of auditory inputs within modality-specific sensory cortex.

Likewise ERP studies on auditory feature selection (e.g., Woldorff, Hansen & Hillyard, 1987) strongly support the early selection models, which suggest a hierarchical selection process during stimulus analysis. The ERPs indicate both an early selection of attended stimuli and a rapid rejection of irrelevant stimuli after an analysis of their salient features as postulated by the central tenet of early selection theory.

In addition to the selective attentional processing of features, processes of automatic feature analysis are also important in auditory perception. An ERP component termed the "mismatch negativity" (MMN) has been identified as an important index of automatic feature analysis in the auditory system (Näätänen, 1992). The MMN is specifically triggered (with a latency of 150-200 ms) by physically deviant sounds in a repetitive sequence. Because the MMN may be elicited by deviants even when the subject's attention is diverted from the sounds (e.g., during reading), it has been suggested to represent an automatic form of sensory analysis. Therefore the brain has to form automatically short-term memory traces of auditory features - this echoic trace may persist for 6-10 sec - against which it can compare the incoming sensory information, for the purpose of detecting changes in the auditory milieu.

The fact that the MMN is observed primarily in the auditory cortex may be an indication for the special importance of detecting changes in the auditory environment - especially in evolutionary terms. These findings as well as other more recent ones indicate that information processing in the auditory pathway is under the control of attentional processes at very early levels.

This very early selection in the auditory pathway could even be interpreted as a maybe crucial and necessary filter, which prevents overloading of the sensory system and allows rapid and efficient processing of critical (maybe even life-threatening) stimuli.

3.4   Visual – Spatial Attention and Feature Selection

3.4.1   Visual-spatial attention paradigms

From a today's cognitive perspective one would say that selective attention can take many forms in visual processing, involving both "early" perceptual and "later" postperceptual processing operations. It is therefore suggested that selection has no unitary locus in the visual system, but rather selection is dependent upon the processing operations performed on a sensory input. In the visual domain, spatial attention refers to the act of covertly attending to nonfoveal locations within the visual field.

In the late 1960s Eason first applied successfully electrophysiological methods to study visual-spatial attention in humans. Eason and colleagues examined ERPs elicited by lateralized flash stimuli when those stimuli were either actively attended or explicitly ignored by the subject. The finding was that the ERPs in the latency range between 100 and 200 ms after stimulus were altered by the direction of attention in the visual fields. The general effect has been that stimuli falling within the "scope" of spatial attention elicit (predominantly) enhanced early P1 (peaking between 80 and 120 msec) and N1 (160 - 200 msec) ERP components over posterior scalp regions. Regarding to Mangun, Hillyard and Luck (1993) briefly flashed visual stimuli like those used by Eason elicit positive and negative components over the posterior scalp that begin as early as 35 - 40 ms poststimulus (!). However, typically only the larger, more prominent of these ERP components (P1, N1, P2, N2) can be readily observed.

To control for the arousal level (or non-selective attention) of the subjects identical physical stimuli are typical compared when attended versus when disattended (see fig. 2).
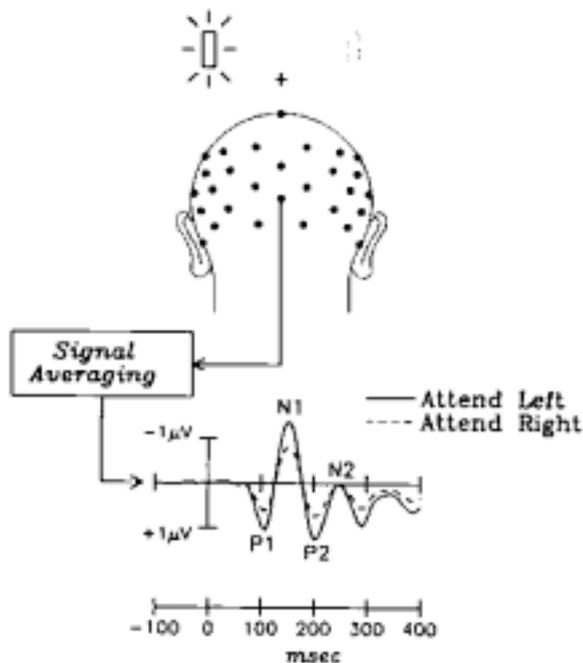
Figure 2. Schematic representation of the visual ERP components in a typical spatial attention experiment. In this example, left and right stimuli are shown being presented one at a time to the left and right visual fields. While continuously maintaining fixation on a central point (+), the subjects are instructed to attend to one stimulus position while ignoring the other; the goal is to detect target stimuli embedded within the sequence of target and nontarget stimuli at the attended location. The effects of attention are most validly assessed by comparing the ERPs elicited by the stimuli at a given position when that position was attended as compared to when attention was directed to the opposite visual field location: ERPs to left-field stimuli are indicated at bottom. The ERP waveform consists of a sequence of positive and negative deflections (components) labeled P1, N1, P2, and N2 (positive is plotted downward). These components are sensitive to the direction of attention and are typically larger in amplitude when the evoking stimulus is attended. Since these ERP components are relatively small in comparison to the ongoing EEG, signal averaging of the responses to many stimulus presentations is required to obtain a reliable waveform.

(from: Mangun, Hillyard, & Luck, 1993)

A different spatial-attention paradigm involves trial-by-trial cueing or priming, in which the cue or prime stimulus indicates the most likely location at which a subsequent test stimuli will appear. Test stimuli presented to the precued (attended) location are usually detected and discriminated faster and/or more accurate than those at unattended locations. Posner's (1980, cited in Posner, 1995) results indicated that focused spatial attention can directly alter the processing of stimulus inputs, which he attributed to improved sensory-perceptual processing at attended locations. Inspired by this research the suggestion arose that spatial attention could be seen analogous to a "mental spotlight" or zoom lens that facilitates the processing of stimuli falling within its focus ("benefit" for attended stimuli) and exerts dampening effects on signals at "unattended" locations ("costs" for unattended stimuli). When considering the neural correlates of spatial attention, a distinction between those brain areas which serve as the source of the attention effect and those which are the site of the attention effect, seem to be helpful. The attentional source involves those structures which are devoted to the "operation of the spotlight" per se (such as moving it from one to another location) and which

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are also mediating the top-down or executive control of the spotlight. The attentional site on the other hand involves those visuocortical areas which are primarily involved in stimulus processing and whose functional activity can be modulated by spatial attention (Handy et al., 2001). Posner (1995) defined the act of attentional orienting as a three-step process; When a subject is cued to switch her spatial attention to a new location, attention must first be disengaged from its current location, then be moved to the new location and finally attention must be engaged with the stimuli within the new location. It is strongly suggested that these operations are performed by different neural structures. The parietal lobe, for example, is thought to be involved in mediating the act of disengaging attention from its current focus, whereas the superior colliculus and related midbrain areas are responsible for moving the attentional spotlight and the pulvinar nucleus of the thalamus is suggested to be the third component responsible for engaging stimuli at the new location.

The consistent finding in all these cueing studies are enlarged P1 amplitudes over visual cortex for validly cued targets and shorter reaction times (e.g., Hillyard, Luck, & Mangun, 1994) (refer to fig. 3).
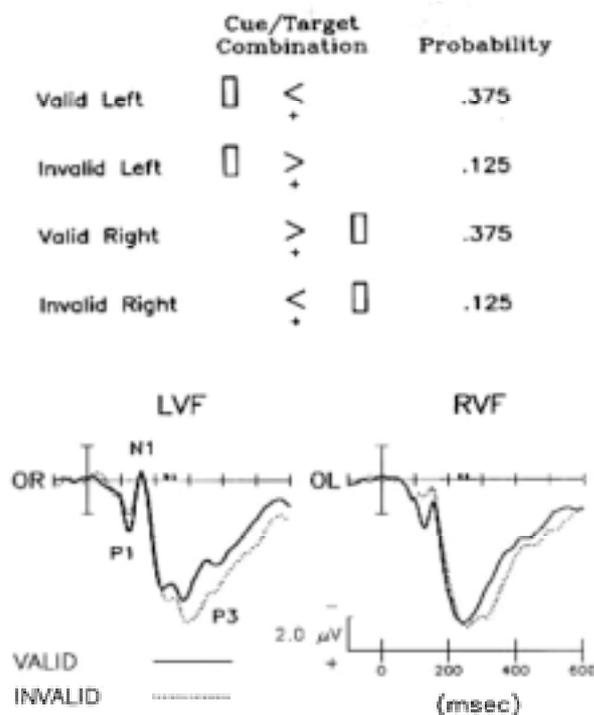
Figure 3. Typical spatial cuing paradigm

Subjects made simple reaction-time responses to both valid (p = .75) and invalid (p = .25) targets. ERPs were averaged separately for valid and invalid targets in the left (LVF) and right (LVF) visual fields. The ERPs shown were recorded from the contralateral occipital scalp (from: Mangun, Hillyard, & Luck, 1993).

All of the ERP paradigms considered so far used experimental designs in which single, isolated stimuli were presented to either the attended or unattended visual field. Taking to

account, that solitary stimuli presented in an "empty" visual field tend to draw attention to their locations rather automatically regardless of whether they are supposed to be attended question if those designs are well suited for studying visual spatial selection. For this purpose multi-element stimulus arrays as that used by Heinze et al. (1990, cited in Mangun, Hillyard, & Luck, 1993) seem to provide better conditions. Early visual ERPs are generally largest over the hemisphere contralateral to the visual field of a lateralized stimulus. Thus, the two hemispheres should be activated approximately equally by a bilateral stimulus, and as soon as attention is guided toward a single visual-field a relative enhancement should occur only in the hemisphere contralateral to direction of attention (fig. 4). That's exactly what happens, but surprisingly the contralateral P1 component was similarly enlarged for both relevant and irrelevant stimuli flashed to the attended side which provides evidence for an early selection process based solely on location (Heinze et al., 1990).
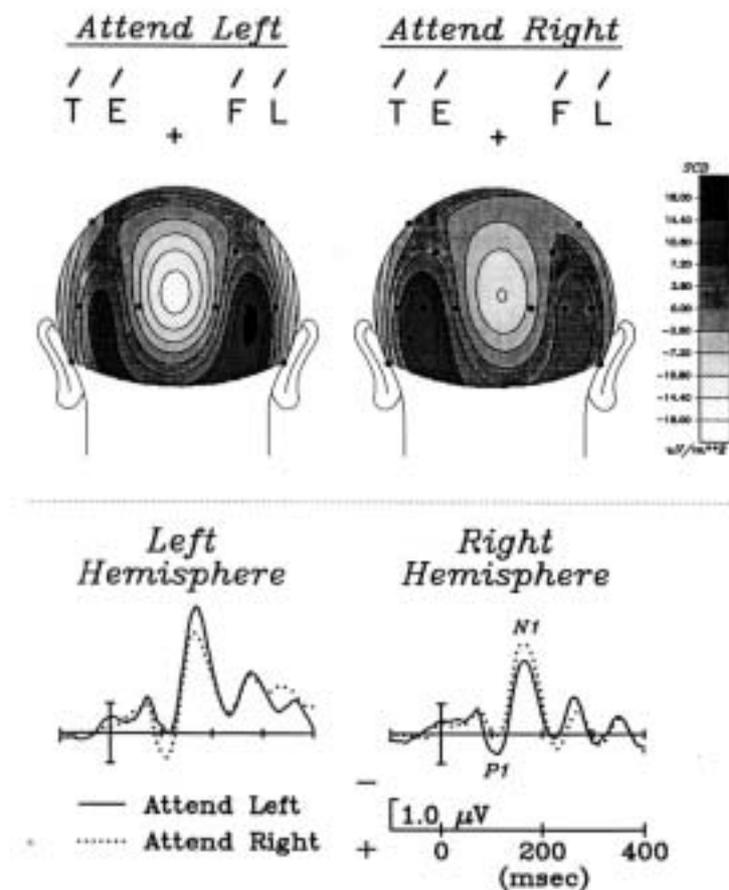
Figure 4. Multielement display

ERPs to sequences of bilateral arrays of letters were recorded while subjects attended to either the left or right half of the display. Note that the P1 wave is larger over the right hemisphere during the attended-left runs and larger over the left hemisphere during the attended-right runs. Topographic maps for CSD for the P1 wave (100 ms) show a strong source over the lateral occipital scalp contralateral to the attended hemifield (from: Heinze, Mangun, & Hillyard, 1990, in Mangun, Hillyard, & Luck, 1993).

The ERP data reviewed so far strongly supports the hypothesis that early selection is a basic property of human visual-spatial attention. It is to be noted that those amplitude enhancements of the early P1 and N1 components are uniquely associated with visual-spatial attention, whereas very different patterns of attention related ERP components emerge when selection is based upon other stimulus attributes such as color, orientation, or feature conjunctions. In these cases the component elicited by attended stimuli is typically a broad "selection negativity" that begins at 140 – 200 msec and lasts over several hundred of milliseconds thereafter. It seems that there indeed exists an order in which selection of different stimulus attributes takes place, starting with location, which seems to have an unique and superior status within visual selection and continuing with contours, which seem to be of similar "importance". Only thereafter "luxurious" attributes like color or orientation are selected and extracted by attentional processes. For example, if spatial selection is combined with a second form of selection, such as attending to both location and color of a stimulus, selection for the nonspatial attribute is hierarchically dependent on whether or not the stimulus was in an attended location; that is selection for e.g., color can only occur for stimuli presented in attended locations.

3.4.2   Enhanced sensory processing or decision bias?

There is plenty of evidence (e.g., Eason, 1981; Mangun & Hillyard, 1990; Hillyard, Luck & Mangun, 1994) suggesting that the larger P1 and N1 amplitudes evoked by attended-locations are signs of improved or enhanced sensory processing or as described by Eason reflecting a type of "gain control" of selective attention mechanisms over sensory/perceptual processing. The modulation on P1/N1 amplitudes is described as the influences of descending (efferent) neural projections onto the sensory neurons. Presumably, at the neuronal level enhancing the excitability of sensory neurons at attended locations are causing those amplified P1/N1 components (Mangun & Hillyard, 1995). The observation that spatial attention modulates mainly the amplitudes of the P1 and N1 components without significantly affecting their latencies, scalp distributions or wave-shapes is consistent with the idea that during different conditions of attention the same sensory neurons are being activated by the stimulus, but that attention modulates sensory/perceptual processing by means of sensory gating or filtering of inputs (Mangun & Hillyard, 1995).

The challenging argument, whether the improved response performance of attended stimuli might be rather due to alterations in decision and/or response bias is addressed by the principal finding that the early P1 and N1 components are constantly larger in peak amplitude

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when the evoking stimulus has been precued. If on the other hand the cueing effects on RT would be a result of changes in decision and/or response bias then one would expect stable early ERP components and instead, changes in the longer-latency components related to decision and action.

Earlier reported findings have been interpreted as evidence and support for Posner's and others proposal that expectancy-induced facilitation of RT and perceptual sensitivity could be the result of improvements in early sensory and perceptual processing.

For example, in the studies of spatial and color attention by Hillyard and Munte (1984) attention effects on ERPs were greatly reduced for stimuli at the unattended location even though some of those stimuli shared a feature (i.e., color) with the defined targets. But if all the elementary features of the stimuli had been evaluated prior to selection – as postulated by late selection theory – one would expect at least some effect of the color cue at unattended locations.

Taken together, the data from spatial and non-spatial attention studies using ERPs indicate that selection by location takes place at an earlier level (manifested as early P1s within 70-100 ms) and involves a qualitatively different mechanism (in the latency range of 150-200 ms) from selection by other stimulus attributes (e.g., color).

3.4.3   Where are those early components located?

Besides that, there also exists some anatomical and functional segregation of the visual pathways with respect to selective attention that have not been mentioned yet. Animal experiments identified separate dorsal and ventral processing "streams" that originate in primary (striate) visual cortex and mediate different aspects of visual perception. The dorsal stream projects to the posterior parietal lobe and is important for encoding the spatial aspects of visual inputs and for guiding visuomotor behavior. The ventral stream, on the other hand conveys information about stimulus form, color, and pattern to the inferior temporal lobe. It could be shown that spatial selective attention exerts strong influence on VEPs in both the ventral and the dorsal streams, but not in prestriate area V2, or the striate cortex itself (e.g., Desimone & Ungerleider, 1989, cited in Mangun, Hillyard, & Luck, 1993).

Moreover for the attention-sensitive P1 component there are several indications (i.e., multichannel mapping or current-source density analysis) that it is generated in the ventro-lateral extrastriate cortex (Brodmann's area 18 and/or 19) (Mangun et al., 1993). However, the earlier C1 component (50-80 ms) or the NP80 component described for example by Clark, Fan, and Hillyard (1995) or Mangun, Hillyard and Luck (1993), respectively are attributed to

striate cortex and seem to be unaffected by spatial attention. Recently, Luck and Hillyard (in Gazzaniga, 2000) postulated again that visual processing is affected by spatial attention as early as 70-80 msec after stimulus delivery (the onset of the P1 wave) and that most likely occurs within extrastriate cortex (encompassing areas V2-V4), which would have explanatory significance as that can be interpreted as evidence that spatial attention can not modulate visual processing before reaching extrastriate cortex. A corpus of evidence not only from human electrophysiology, but also from neuroimaging techniques measuring hemodynamic responses (PET, fMRI) strongly support the notion that spatial attention can affect processing not before extrastriate visual cortex.

In contrast the N1 wave is of maximal amplitude over parietal scalp sites for stimuli at attended locations (e.g., Mangun & Hillyard, 1990). The dissociation of the P1 and N1 components observed in different task conditions raise the possibility that they might indicate the operation of two different attentional systems. Hillyard, Luck and Mangun (1994) associated the suppression of the P1 component with "attentional costs" and suggest that this effect may be a sign of an predominantly inhibitory process that is applied to inputs coming from unattended locations during focal attention. Similarly, they associate posterior N1 enhancement with "attentional benefits" and state that this may be a sign of a complementary process that enhances perceptual processing for the location which is at the focus of attention (see fig. 5).
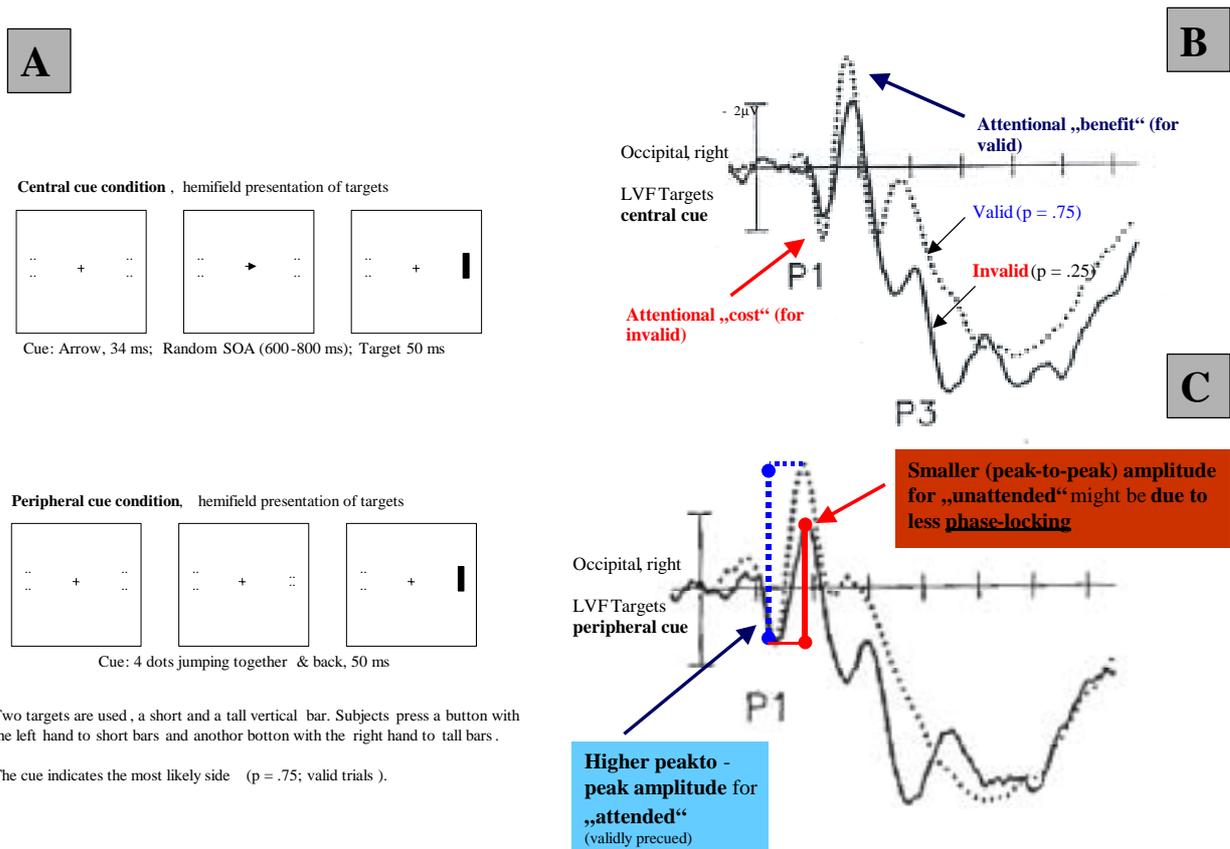
Figure 5. Schematic figure showing attentional cost and benefits in a spatial cuing task

A: Comparison between central and peripheral cues. Left visual field (LVF) presentation of targets (occipital right). **B:** Central cue condition. Note augmented P1 amplitude for invalid and N1 enhancements for valids, reflecting attentional "costs" and attentional "benefits", respectively as suggested by Hillyard, Luck, & Mangun (1994). **C:** Peripheral cue condition. Alternatively, higher peak-to-peak amplitudes might indicate enhanced phase-locking. (Modified from: Hillyard, Luck, & Mangun, 1994).

3.5   ERP modifications due to "sustained attention"

As more sustained attention and deeper attentional involvement is related positively to hypnotizability (for review, see Crawford & Gruzelier, 1992), it was postulated that it also may be reflected neurophysiologically in either the amplitude or latency of certain ERP wave components. Dragutinovich and Sheehan (1986, cited in Crawford & Gruzelier, 1992), for example, found significantly shorter P200s and larger amplitudes in high hypnotizables (to visual stimuli) and suggested that this may reflect the greater attentive involvement among "highs" when instructed to attend to visual stimuli. In another study of selective attention, a dichotic listening task, Crawford, Corby, and Kopell (1996) found also interesting hypnotizability-related differences in N1 components. As they increased the intensity of the tones (50-, 60-, 70, and 80-dB), low hypnotizables decreased their N1 latencies, whereas highs increased their N1 latencies. Thus, highs appeared to process distracting stimuli – which

they were instructed to ignore – more slowly than lows, which could be interpreted as a greater (attentional) control ability of highs over their cognitive processing.

It is also well documented that highs can completely eliminate the perception of pain – probably through frontal inhibition – while physiological reactivity is still evidenced (e.g., Crawford et al., 1998). During hypnotic analgesia to pain-stimuli, alterations in P100s – signal detection – as well as in P300s – cognitive awareness of the incoming stimuli – can be observed.

Plenty of evidence has been presented to support the idea that attention can indeed modulate early sensory and perceptual processing. It remains however unresolved whether auditory and visual modalities differ in the cortical level at which earliest selection takes place.

The consequence of these early selection mechanisms are that inputs to higher perceptual and cognitive process are already altered (or pre-filtered), and thus selective attention powerfully influences our perception and awareness of the world around us.

4   Brain oscillations

The core philosophy for measuring "induced rhythms" is described as follows (Gray et al., 1992, cited in Basar, 1998): If an electrode happens to be above a structure responsive to sensory stimuli, the presentation of a stimulus will evoke a sustained rhythmic fluctuation of potential outlasting the stimulus. "This propensity for neural structures to generate oscillatory waves of activity has come to be termed an 'induced rhythm'. It is a general property of sensory, as well as many other neuronal networks that is expressed during periods of activation" (p. 148). Given this very basic predication I am going to suggest an alternative model for the generation of event-related potentials (ERPs). By doing so I try to overcome the big gap between ERPs and brain oscillations and will argue that there is indeed a substantially closer bond between those two as most researcher would expect and/or accept.

4.1   An alternative model for the generation of ERPs

A completely different model for explaining the generation of ERPs is that first suggested by Sayers et al. (1974) and today supported by many others (e.g., Basar, 1997; Polich, 1997; Brandt, 1997). This model basically assumes, that ERPs result from reorganization of already existing ongoing EEG-activity. In other words, every evoked potential may contain oscillatory responses in various frequency ranges depending on information processing demands. For example, it was already shown that most of the powerful and large amplitudes in human sensory evoked potentials lie in the theta and/or alpha frequency range (Basar, 1998). By applying suitable stimuli it, therefore appears to be possible to have the brain react with distinct oscillations. For example, Schürmann et al. (1995, cited in Basar, 1998) showed that the P300 response is predominantly a response in the delta frequency range.

The basic idea of oscillatory brain activity reorienting and becoming phase-locked in response to a stimulus is depicted in figure 6.
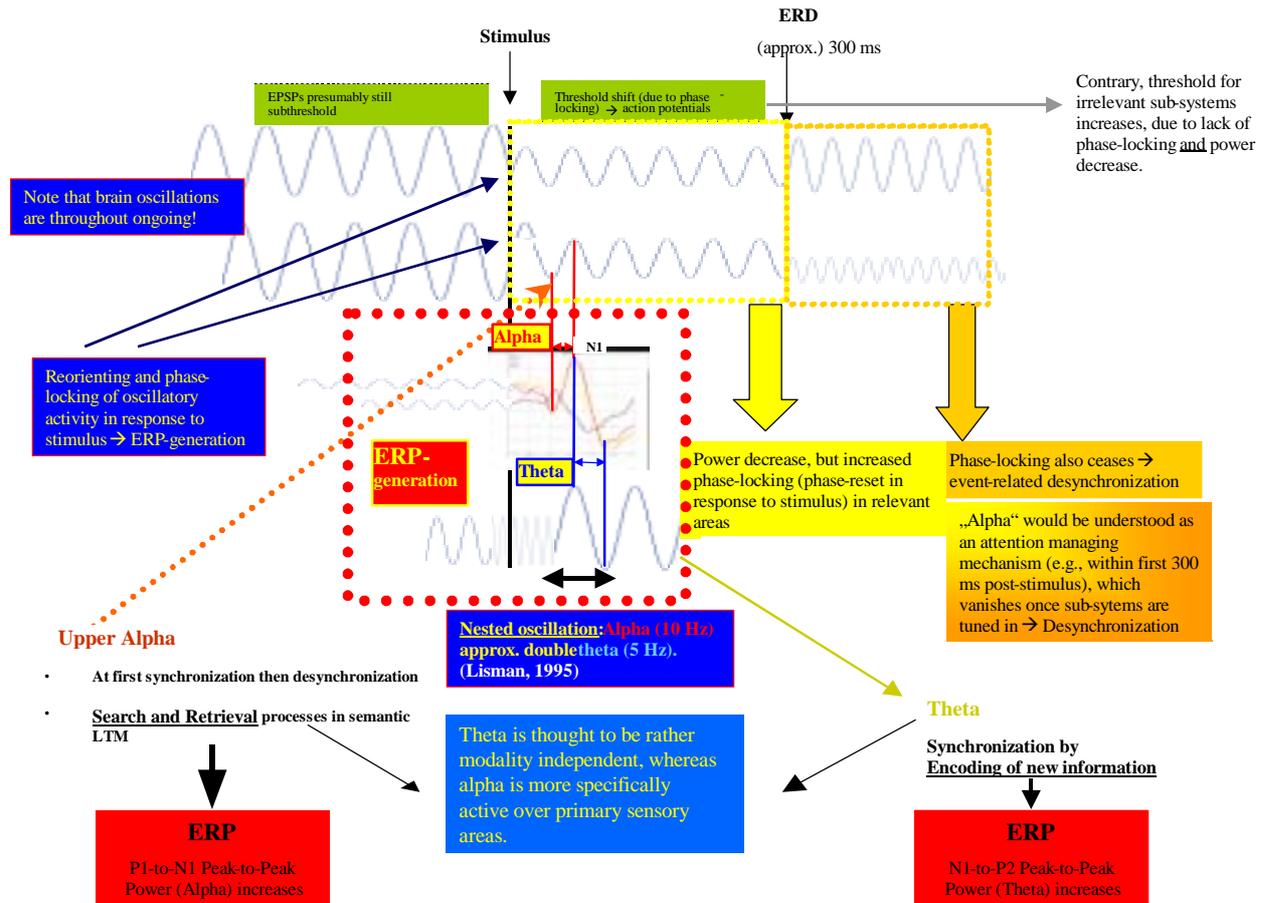
Figure 6. Phase-locking and the ERP. An alternative model

The figure schematically highlights the interplay between brain oscillations (alpha, theta) and event-related potentials (see red dots). Furthermore, the complex interaction of event-related alpha desynchronization (ERD) and phase-locking is shown to encounter possible contradictions, presumably arising as we go on to experimental sections. Ganzseitige FIGURE!

The classical assumption of the additive "averaging-method" is that EEG activity not time-locked to an event will vary randomly across epochs and therefore this "background EEG" will tend to average to zero, whereas neuronal populations becoming active in response to a stimulus are being summed up and show up as ERPs. Considering that, one has to think seriously about the meaning of the traditional term "signal-to-noise ratio" commonly used in ERP-research.

This notion that ERPs are nothing more than the sum of deterministic signals with uncorrelated background noise was at first questioned by results obtained from Sayers et al. (1974), which showed the interdependence between ongoing neural activity and stimulus-induced activity, which led to a reorganization of the latter. Accordingly, Basar (1980, p. 32, cited in Basar, 1998) argues that: "The spontaneous activity is not simply a noise, but a kind of controller which affects the production of signals (or at least, which affects the conduction of signals) in the brain...". We will discuss this alternative approach in subsequent sections more in detail, as it provides the necessary framework for this whole research project.

4.2   <u>Analysis in the "frequency-domain"</u>

In the frequency domain a variety of different measures such as event related desynchronization (ERD), spectral coherences (Petsche and Rappelsberger, 1992) or special methods of frequency domain analyses of ERPs (e.g., Basar et al., 1992, 1997) are used. Although the interest for analysis in the frequency-domain (and alpha activity) declined from the late 1960s on, it is again being paid more attention to, as for example reflected by Näätänen (1992, p. 75): "Some recent developments in the field, for example those involving event-related desynchronization patterns of the EEG rhythms on the scalp (e.g., Klimesch, Pfurtscheller, & Mohl, 1988; Pfurtscheller & Klimesch, 1991), indeed indicate that the ongoing EEG may serve as an important tool for cognitive brain research". Or as Rugg and Wilding (2000) put it: "In addition to the measurement of item-related neural activity, electrophysiological methods can be used to investigate state-related activity extending across experimental trials. This can be achieved by analysis of the frequency characteristics of inter-trial epochs of the 'background' EEG (Klimesch, 1999)".
Several experiments linking oscillatory brain activity to specific cognitive processes are supporting the notion that neuronal information-processing is dependent or based upon brain oscillations (e.g., Klimesch, 1996; Weiss & Rappelsberger, 1996; Pulvermüller, 1999; Basar, 1997; Lisman & Idiart, 1995; Herrmann, 2000).

By using the ERD- and IBP-methods for EEG-analysis Klimesch (1996, 1999) could demonstrate quite distinct functional correlates (e.g. general arousal, expectancy, retrieval, stimulus encoding) even for very narrow frequency-bands (being only 2 Hz apart). "Induced band power" (IBP) reflects induced oscillations (see also Bullock, 1992) that are modulated by stimuli or events and which (in contrast to evoked rhythms) do not respond in a phase locked manner or are independent of phase locked EEG activity. Under conditions where phase locked activity is lacking, event-related bandpower (ERBP) equals IBP. On the other hand, in cases where phase locked activity is large, IBP will be much smaller than ERBP. This allows to determine whether and to what extent phase locked activity influences certain ERP components. Refer to fig. 7 for a depictions of event-related EEG oscillations, commonly divided into

a.) phase locked "evoked" activity (ERD or ERBP, ERP)
b.) non-phase locked "induced" activity (ITV or IBP)
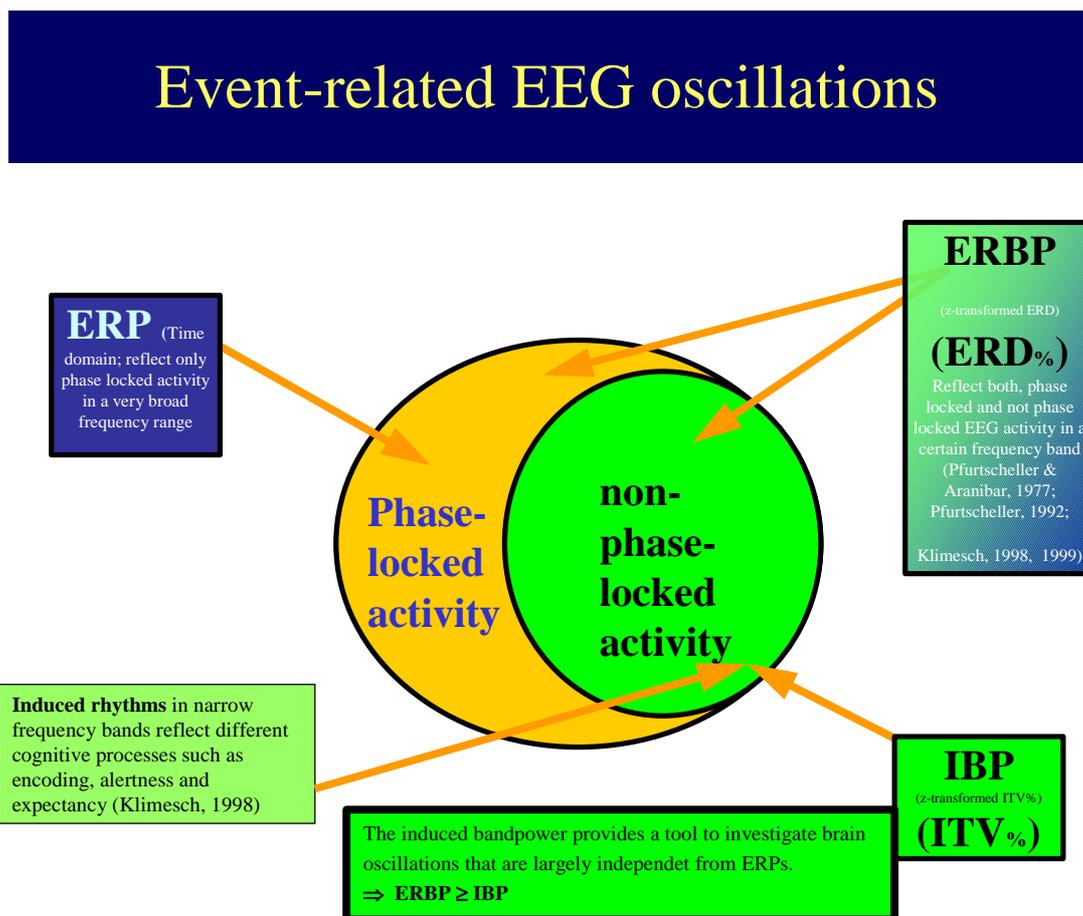
Figure 7. Overview of event-related EEG oscillations

ERP (event-related potentials), ERBP (event-related bandpower), ERD (event-related desynchronization), IBP (induced bandpower), ITV (intertrial variance). ERPs capture only phase-locked (evoked) activity, whereas ERBP (ERD) also capture non-phase locked (induced) activity. Evoked activity can be understood as "phase-reset" oscillatory activity, whereas induced activities are reflecting "stimulus-modulated" or "phase-modified" oscillations (Modified from: D. Röhm, personal communication, May 2001).

4.3   <u>Alpha oscillations</u>

Since the early discovery of the alpha rhythms by Hans Berger, the biggest puzzles remaining have been (1) the physiological understanding of their origin, (2) their relation to sensory and cognitive functioning of the brain, (3) and lastly the interaction of those two.

> If one understands the alpha rhythm, he will most probably understand the other EEG phenomena (Storm van Leeuwen, 1979, as cited in Basar, 1997).

In the following I will try to stress the functional significance of alpha activity which consequently should weaken the old concept of alpha activity as a predominantly passive state of the central nervous system or the "idling" of the brain.

An overview of the most important EEG-Phenomena (in the alpha range):

1. **Ongoing (spontaneous) EEG**

    Alpha waves, sleep spindles, spike activity in epilepsy,…

2. **Event-related changes in oscillatory activity**
    - Alpha can be <u>emitted</u> or locked to a future moment. That means, that well trained subjects emit time-locked bursts of alpha band energy for up to a second before the delivery of an expected target (Basar et al., 1992)
    - Alpha rhythms can be <u>evoked</u>, i.e. precisely time-locked to a stimulus (Basar et al., 1992)
    - Alpha rhythms can be <u>induced</u>, i.e. initiated by, but not closely time-locked to a stimulus (Basar et al., 1992)
    - Alpha can be <u>movement-related</u> and also <u>memory-related</u> (Pfurtscheller and Klimesch, 1992)

4.3.1   Ongoing (spontaneous) EEG

The so-called spontaneous (ongoing) alpha activity around 10 Hz can be recorded primarily during wakefulness over posterior electrode sites under conditions of physical relaxation and mental activity, with eyes closed. Alpha frequency is faster over posterior and slower at anterior recording sites (for review, see Niedermeyer, 1999).

4.3.2 Emitted Alpha

Rather than being merely noise alpha activity are functionally relevant signals and should be thought of as "a manifestation of internally cognitive evoked potentials as signs of expectancy and short term memory" (Basar, 1997, p.6). That means that prestimulus EEG becomes phase-locked to an expected target (emitted alpha), or as described by Schürmann et al. (1997) the transition-effect from a "disordered" to an "ordered" state of the brain.

Best examples for the quasi-deterministic nature of "spontaneous alphas" postulated by Basar (1997) is the following experiment demonstrating the phase-locked and reproducible 10-Hz pattern preceding cognitive targets. In an experiment by Basar et al. (1997) subjects heard tones of 2000 Hz, 80 dB, and 800 ms duration in regular intervals of 2600 ms. Every third or fourth tone was emitted and subjects were asked to predict and to mark mentally the time of occurrence of the omitted signals. Regular, phase-ordered pre-stimulus EEG-rhythms could have been observed, which tended to form repeatable patterns preceding successful cognitive tasks. As the superimposition depicted in fig. 8B (end of experiment) shows, the amplitude increase observed in the average (fig. 8A) is not only due to alpha amplitude increase in single trials but due to increased synchronization of alpha waves (see fig. 8).
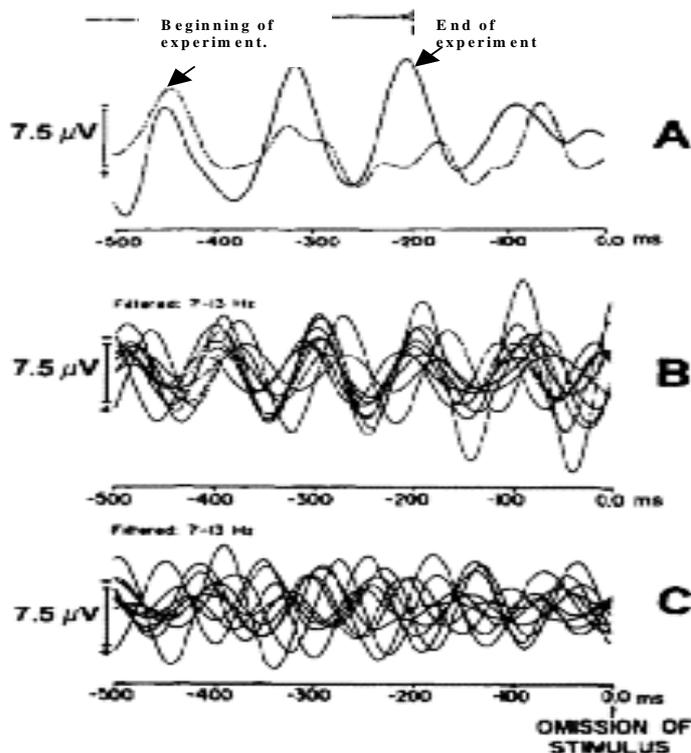
Figure 8. Anticipatory 10-Hz oscillation („Emitted Alpha") phase-locked to the appearance of a cognitive target

Figure shows vertex recordings (digitally filtered: 1-25 Hz) of averages of the first and last 10 pre-stimulus EEG-segments (**A**), as well as averages of the first (**C**) and the last (**B**) 10 pre-stimulus EEG-epochs, separately. Note the regular rhythmic, high amplitude behavior at the end of the experiment (**B**), as opposed to the less regular and low amplitude oscillations of the first 10 sweeps (**C**), where the subject still "felt uncertain about stimulus timing" (Modified from: Basar, 1997).

4.3.3 Evoked Alpha

In response to application of sensory stimulation the brain commonly responds with short 10-Hz oscillatory behavior with a duration of approx. 300 ms upon stimulation, termed "evoked alpha" (Schürmann et al., 1997, Basar et al., 1992). Though, as stated by Schürmann et al. (1997, 2000) inadequate stimuli cannot generate significant and time-locked cortical alpha enhancements in the first 300 ms after stimulation. The occipital cortex of the cat brain, for example does not oscillate (or is strongly weakened) with enhanced 10-Hz if the stimulation is an auditory one (refer to fig. 9).
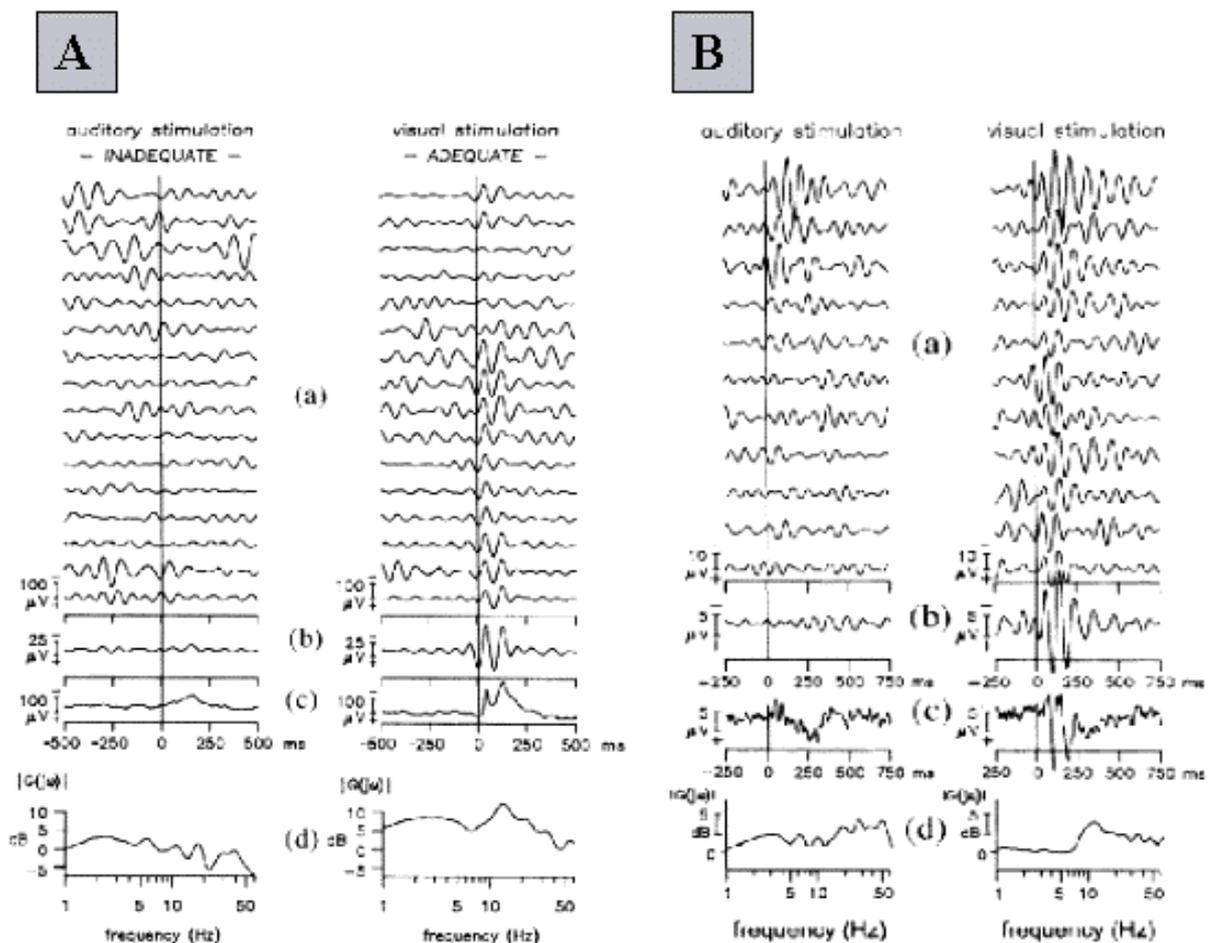
Figure 9. Evoked alpha rhythms recorded with intracranial electrodes in the cat brain (visual cortex, area 17) (A) **and on a human scalp** (occipital) (B)

On the left each time with inadequate, i.e.: acoustical stimuli, on the right, with adequate, i.e.: visual stimuli. (a) Filtered single trial EPs (8-15 Hz). (b) Filtered averaged EP (8-15 Hz). (c) Wide-band filtered averaged EP. (d) Amplitude frequency characteristics computed from averaged EP (from: Schürmann & Basar, 2001).

According to Basar (1997, p.25) "Cortical and thalamic 10-Hz responses can be elicited only by stimulations that are adequate for the respective area. In contrast, hippocampal 10-Hz responses are present in all types of stimulations". Furthermore, the group around Basar postulates that the hippocampus reacts with an ample 10-Hz oscillatory behavior around 9-10 Hz upon auditory and around 12 Hz upon visual stimulation (see fig. 10).
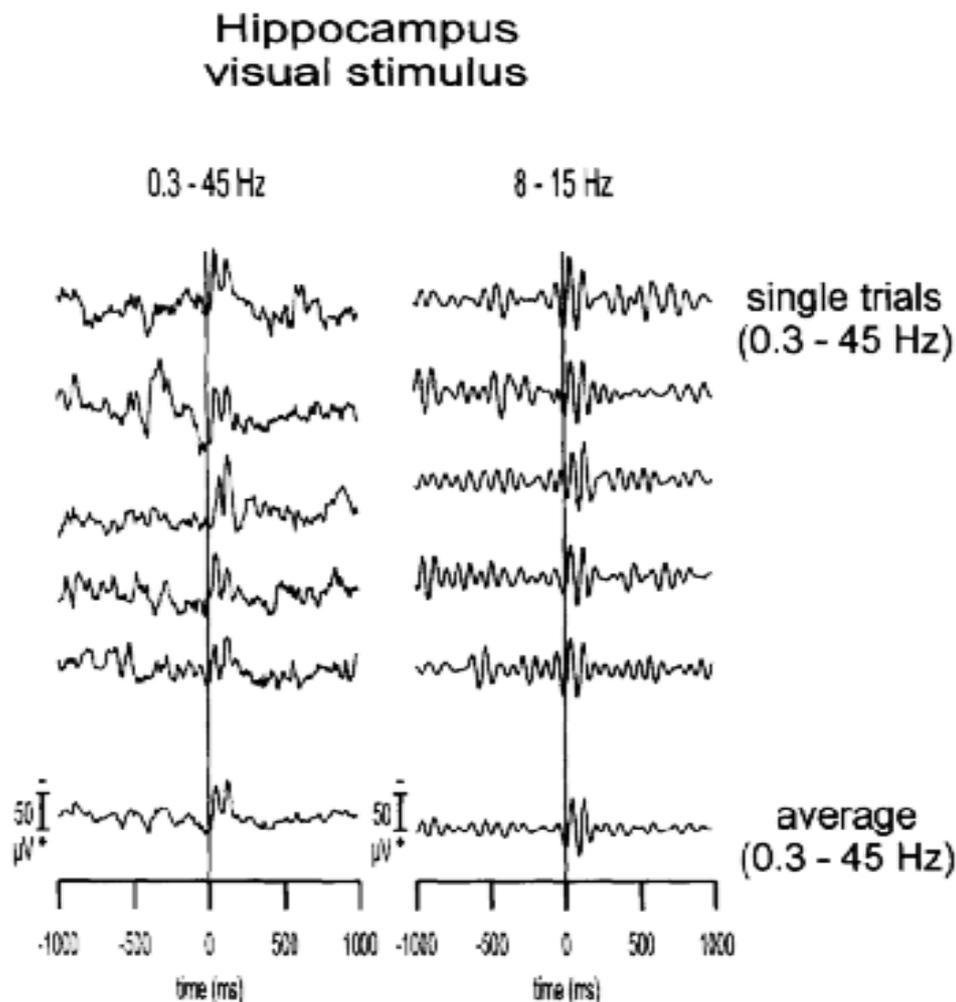
Figure 10. Strong resonant alpha response of 12 Hz upon visual stimulation in the hippocampus of the cat

Above, single trial EPs; below, averaged EP. On the left, wide-band filtered responses (0.3-45 Hz), on the right, responses filtered in the alpha range (8-15 Hz). Note the distinct alpha responses in the first 200 ms after stimulation which are visible even on wide-band filtered single trial basis.

4.3.4   Induced Alpha

Besides being externally triggered due to sensory stimuli and then shifting to coherent states of EEG activity, the brain is also capable of synchronizing its oscillations in response to internal proprioceptive, or internal cognitive processes. Or in other words, if the brain is brought to a state of excitation, either by means of sensory stimulation or cognitive tasks, it's

capable of generating induced alpha rhythms. Note that oscillations that are modulated by stimuli or events and which (in contrast to evoked rhythms) do not respond in a phase-locked manner are termed "induced rhythms" (as schematically shown in fig. 11).
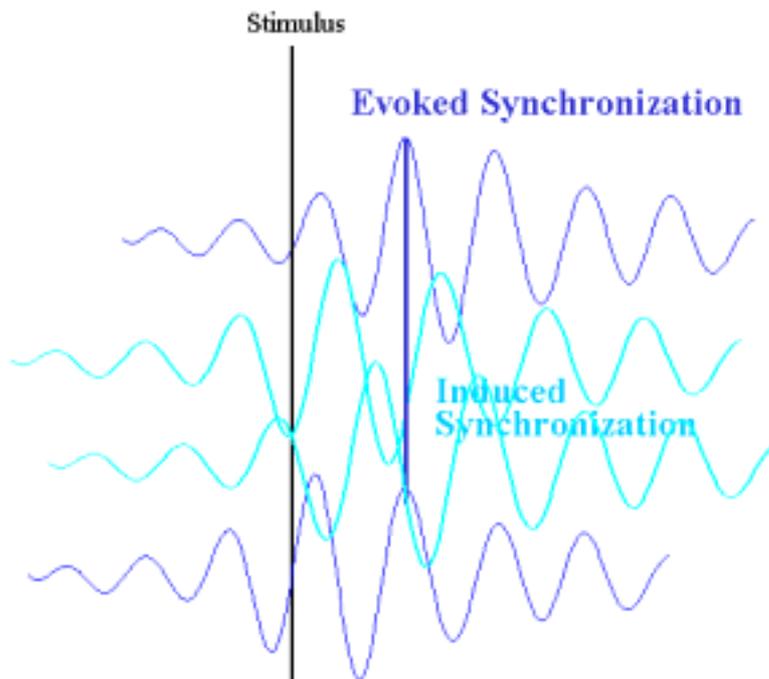
Figure 11. Schematic description of evoked and induced activity

The conventional measure of band power, which consists of evoked and induced components, is termed event-related bandpower (ERBP). The IBP-measure (induced band power) is deprived from phase locked EEG activity and reflects „induced rhythms" (oscillations) that are modulated by stimuli or events and which do not respond in a phase locked manner (from: W. Klimesch, personal communication, May 2001).

4.3.5   Movement and memory related alpha

Rolandic (central) mu rhythm is in frequency and amplitude related to the posterior alpha rhythm, but its topography and physiological significance are quite different. The mu rhythm (mu stands for motor) appears over the motor area and desynchronizes (becomes suppressed) during motor related task demands (for review, see Pfurtscheller, 1999).

Klimesch et al. (for review, see Klimesch, 1999) presented evidence that ERD in the upper alpha band reflects semantic or long-term memory processes, whereas event-related desynchronization in the lower alpha band appears to be related to attentional demands. Upper alpha desynchronization is topographically restricted, whereas lower alpha desynchronization is obtained in response to almost any type of task and is topographically widespread over the entire scalp. The focus of upper alpha band ERD during visually presented information, for example, lies above parieto-occipital areas (Pfurtscheller, 1999). For details on ERS (event-related synchronization) and ERD also proceed to section 4.5.

The rationale of the following assumptions are recent developments in the field of the integrative neurosciences, and human electrophysiology (Basar, 1997):

- Methods of chaos analysis support that "spontaneous" 10-Hz activity is not pure noise, but probably a signal with quasi-deterministic (showing "recurrently emitted EEG patterns") properties.

- Evoked 10-Hz oscillations can be generated in several structures of the brain simultaneously. The damped oscillations (of approx. 200-300 msec duration) after sensory stimulations are further sensitive to the modality of stimulations and recording site.

- 10-Hz spontaneous rhythms and evoked rhythms are distributed in the human brain, in the brain of animals, and even in the isolated ganglia of invertebrates.

- Furthermore, spontaneous and evoked 10-Hz oscillatory activities are also recorded at the cellular or membrane level, thus demonstrating the physiological origin of these "alpha"-oscillations (see section 4.4.1).

4.4 <u>Is there a unique pacemaker or generator for the alpha rhythm?</u>

Data obtained at the cellular level from Steriade (1990, 1999) and the group around Llinas (e.g., 1988) might favorite thalamic pacemakers for alpha activity, whereas Basar and Schürmann (e.g., 1996) are confident that thalamo-cortical circuits are not unique in generating alpha responses.

Rather than assuming a unique alpha generator Basar and Schürmann (1996) or Schürmann et al. (1997) assume a diffuse and distributed alpha system - extending the original idea by Andersen and Andersson (1968) of alpha pacemakers and an interplay between thalamus and cortex - to other structures including brainstem and hippocampus. But it was also demonstrated by Basar in 1972, that upon stimulation an increased coherence in the 10-Hz range between all structures involved in the stimulus processing can be observed, suggesting a central or common mechanism which puts all these various structures into a state of alpha rhythmicity.

Considering the switch from a type-1 oscillation to a type-2 oscillation during mental activity with each subpopulation oscillating isolated but still synchronously - as many different processes have to go on during a cognitive task– seems appealing (as proposed by Klimesch, 1996; cf. Ch. 4.5 and fig. 12). Assuming several alpha-generators which are

distributed in the brain may lead us to the idea that 10-Hz processes are possibly facilitating association in the brain. Or in other words, as a sensory or cognitive input elicits "alpha-wave-trains" in several neuronal structures, those could be understood as a general communication signal or kind of "binding mechanism" between different brain structures.

Models of Lopes da Silva et al. (1997) support the existence of distributed alpha networks with similar design in the brain or as he puts it: "Most likely, alpha rhythms recorded with gross electrodes correspond to complex signals that result from mixing signals arising from different alpha source generators…" (p. 12).

4.4.1   Alpha oscillations at the cellular level

Advances in measuring 10-Hz oscillations at the cellular level made it possible to show oscillatory behavior even at this basic level.

- Dinse et al. (1997) recorded action potential sequences in cats and observed low-frequency oscillations (LFOs) e.g., with a peak in the 8-10 Hz frequency range for visual cortex neurons stimulated by visual stimuli. The maximal observed length of these oscillations can be 500-600 msec (with 7-8 peaks) and might extend the temporal range of info available in neural activity. Given the time-locked nature of those action potential sequences, the authors also find it conceivable that the LFOs reflect a cellular correlate of scalp recordable EEG.
- According to Llinas (1988) thalamic neurons may generate APs at frequencies of 6 or 10 Hz and thereby attributing these phenomena to intrinsic membrane properties (rather than synaptic interaction).
- In addition to those studies, Schütt and Basar (1992, as cited in Basar, 1997) report 10-Hz oscillations at the cellular level in isolated invertebrate ganglia.

For reviews on neural mechanisms underlying spontaneous rhythmic brain activity, see Lopes da Silva (1999) and Steriade (1999).

4.5   Functional Meaning of EEG Synchronization and Desynchronization

In the subsequent section I am going to discuss the "event-related desynchronization" approach (Pfurtscheller & Aranibar, 1977), as well as other electrophysiological work by Klimesch and colleagues with the goal to provide the necessary background on which the experimental work presented at the end of this paper can be better understood and interpreted.

EEG desynchronization (or blocking) of alpha band rhythms due to sensory processing or motor behavior is a long known phenomenon (e.g., Berger, 1929). This desynchronizations can be long-lasting (tonic) or short-lasting (phasic). Phasic desynchronization is related to an internally or externally-triggered event and known as Event-related desynchronization (ERD; Pfurtscheller and Aranibar, 1977). When a primary cortical area receives no or little input from its thalamic gate, it starts to oscillate predominantly in the alpha frequency at relatively high amplitude which is considered to reflect a state of cortical idling (Pfurtscheller, 1996) (see also fig. 14A). Event-related desynchronization, is characterized by its fairly localized topography, its phasic behavior and its frequency specifity (Pfurtscheller, 1999). Attentional and semantic memory demands e.g., lead to a selective suppression of alpha in different subbands. Likewise, Steriade, Jonas and Llinas (1990) suggest EEG desynchronization as a reliable correlate of increased cellular excitability in thalamocortical systems during cortical information processing, which is widely accepted (refer to fig. 12A).

It is a broadly accepted assumption that oscillations are a basic form of communication between cortical cell assemblies. "It is assumed that synchronous oscillations of large cell assemblies – termed type 1 synchronization – reflect a resting state or possibly even a state of functional inhibition" (Klimesch, 1996). During mental activity, on the other hand, different neuronal networks may start to oscillate with different frequencies, though each network may still oscillate synchronously – termed type 2 synchronization; but as a consequence the large scale type 1 oscillation disappears. Klimesch (for review, see Klimesch, 1999) argues, that these different types of synchronizations can be observed in the scalp EEG by calculating event-related power changes within comparatively narrow but individually adjusted (!) frequency bands.

It is a simple but important fact that only if a very large population of neurons oscillate with the same phase and with the same frequency a pronounced rhythmic type 1 alpha activity can be recorded in the EEG. The idea that in response to a cognitive demand, different alpha subpopulations begin to shift their frequencies seems to be interesting. As many different processes have to go on during a cognitive task, it is important to consider the switch from a type 1 oscillation to a type 2 oscillation with each subpopulation oscillating isolated but still synchronously. Note that it is well known and documented that EEG alpha activity is blocked or attenuated by attention and mental effort. See figure 12A. for a comprehensive schematic representation of the "Alpha Paradox" (Klimesch, 2000), as well as of evoked and induced alpha activity.

„The Alpha Paradox" (Klimesch, 2000)

Decrease in alpha power
(compared to reference)
AND
simultaneous synchronization of alpha phase.

A

Brain in „idling"-modus (type-1 synchronization). Synchronous oscillation of large cell assemblies block information processing (Klimesch, 1996)

Shift to type-2 synchronization : Each network oscillating synchronously, but isolated. → Collapsing into subbands (see below).

Cortical areas which are involved in task desynchronize (ERD). → Amplitude of alpha oscillation suppressed.

Evoked Alpha (phase-locked to stimulus)

Showing temporary increase in evoked (phase-locked) activity

Induced Alpha

IBP (induced band power) is deprived from phase locked EEG activity and reflects „induced rhythms" (oscillations) that are modulated by stimuli or events and which do not respond in a phase locked manner (Kaufman et al., 1989, Kalcher & Pfurtscheller, 1995)

B

Setting Individual Frequency Bands

✓ Frequency bands are being individually adjusted by using mean peak frequency during (eyes closed) resting as cut-off point to separate lower and upper alpha.

✓ Definition of frequency bands by using IAF as an individual anchor point (2 Hz steps):

Theta	(IAF – 6 Hz) to (IAF – 4 Hz)
Lower-1 Alpha	(IAF – 4 Hz) to (IAF – 2 Hz)
Lower-2 Alpha	(IAF – 2 Hz) to (IAF)
Upper-1 Alpha	(IAF) to (IAF + 2 Hz)

Distinct frequency bands and their functional correlates

➔ **Theta**
• Synchronization by „Encoding of New Information" (creation of a new code; episodic memory performance)
• Increase in theta power as a function of working memory load (correlated with task demands)

➔ **Lower1-Alpha**
• „phasic alertness"
• general alerting effect, focused appearance during warning stimulus only

➔ **Lower2-Alpha**
• „tonic expectancy"
• general tonic task related attentional demands

➔ **Upper Alpha**
• „Sensory (-Semantic) Long-Term Memory Demands"
• Desynchronization by search and retrieval processes in semantic LTM

Attentional demands

Partitioning of the alpha band into subbands (Klimesch et al., 1993, 1994)

Figure 12. Schematic representation of the "Alpha Paradox" (Klimesch, 2000)

A: If the inhibition to a thalamic gate ceases (e.g., due to sensory stimulation), the input is put through and the alpha oscillations of the respective primary cortical area are suppressed in amplitude while their phase is reset. This leads to the paradoxical effect that evoked (phase-locked) alpha activity increases, whereas simultaneously induced (non phase-locked) alpha activity decreases (Klimesch, 2000). Thus, it can occur that although ERD (power decrease) is observed, evoked potentials suddenly come out due to the superposition of "evoked rhythms". **B**: Setting individual (narrow) frequency bands and their suggested functional correlates. How to define the individual alpha frequency (IAF) for individually adjusting the frequency bands is reviewed in Klimesch (1999).

It were Pfurtscheller and Aranibar in 1977 who first defined a measure for alpha desynchronization and synchronization, terming it event-related desynchronization or ERD (for a comprehensive overview see Pfurtscheller, 1999). "ERD is defined as the percentage of a decrease or increase in band power during a test interval with respect to a reference interval which typically is the timer period within a single trial (epoch) preceding the presentation of a warning signal" (Klimesch, 1996, p. 64).

The most basic finding of this method is that those cortical areas, which are involved in the processing of a task, tend to desynchronize, whereas others show no power change at all or

even synchronize. For example, there is ample evidence that alpha desynchronization is a topographically restricted phenomenon which may reflect attention (e.g., Mulholland, 1969, cited in Klimesch, 1999).

Klimesch further postulates that the resting alpha frequency is created by the overlap of two differing alpha bands, an upper and a lower alpha band. This differentiation seems to be justified as those bands vary largely independent from each other, with the upper alpha band responding selectively to stimulus encoding, whereas the lower alpha band reflects more likely attentional processes and therefore responds to task difficulty (e.g., Klimesch et al., 1992, 1993, 1996). Klimesch, for example, strongly suggests to use individually the alpha peak frequency (alpha as the dominant frequency in the human EEG of adults is manifested by a "peak" in spectral analysis) during resting as cut-off point to separate lower and upper alpha, although the field as a whole has not yet pursued this approach. Regarding to Klimesch (1996), individual alpha frequency (IAF) is directly related to attentional demands and/or memory performance and a decrease in IAF always is related to drop in performance. It's well documented that alpha peak frequency decreases with age, in response to neurological diseases or even due to a lack of school education or mental training. Furthermore, alpha frequency is dependent upon brain volume with smaller brains having presumably shorter feedback loops and therefore faster frequencies, as well as dependent upon other factors like the density (interconnections) of the neuronal net.

Mean peak frequencies of the dominant EEG frequency in the alpha band frequently show double-humps, which probably are an indication of the two overlapping alpha bands or a superimposed faster oscillation (e.g., around 20 Hz) over the slower alpha.

EEG-analysis with the ERD, ERBP and IBP method clearly show that different frequency-bands with a very small bandwidth reflect fundamentally different cognitive processes (e.g. Basar, 1998; Klimesch, 1990, 1997), though it must be emphasized that they can be only functionally distinguished if the frequency bands are being individually adjusted as suggested by Klimesch (e.g., Klimesch, 1999) (see fig. 12B).

If the lack of desynchronization in the lower alpha band reflects low task involvement and non-task related attention or a lack of alertness and attention in general, as postulated by Klimesch et al. (1992), this would validate observed differences between low and high sustained attention participants. These notion is supported by studies of Crawford (1995) who found that in contrast to participants with high sustained attention, those with low sustained attention and difficulty inhibiting distracting environmental stimuli, indeed show a significantly larger proportion of lower alpha power, particularly in the posterior regions of

the brain. The ability to focus attention while inhibiting responses and distractions is a function of the prefronto-limbic attentional system and is fundamental for efficient attentional control and cognitive functioning.

Furthermore, it was shown that EEG frequencies vary interindividually to a great extent, whereas they stay constant within a participant. These evidence taken together supports the notion that different EEG frequencies (within a narrow frequency window) reflect different types of cognitive processes, with possibly different neuronal generators involved in their production.

The use of tonic and phasic (event-related) bandpower changes is based on rich empirical evidence (reviewed in Klimesch, 1999) which demonstrates that EEG oscillations in the alpha and theta band reflect cognitive and memory performance in particular if a double dissociation between the type of EEG response (tonic versus phasic) in two different EEG frequency ranges (in the alpha and theta range) is taken into account. This double dissociation is given by two facts. First, it is well known that with increasing task demands, phasic band power increases in the theta but decreases (desynchronizes) in the alpha frequency range. Second, the extent of a phasic (event-related) EEG response depends at least in part on the extent of tonic power but in opposite ways for the theta and alpha frequency range. Whereas small tonic theta power enhances theta synchronization, large tonic alpha power enhances alpha desynchronization. This relationship is shown schematically in figure 13 and allows to distinguish ‚standard' from ‚best' cases in each frequency band. Klimesch et al. have postulated that the theta band reflects the encoding of new information whereas the lower alpha band is related to attentional and the upper alpha band to semantic processes. Klimesch (1999) suggests that encoding of new information might be reflected by theta oscillations in hippocampo-cortical feedback loops, whereas search and retrieval processes in (semantic) long-term memory are reflected by upper alpha oscillations in thalamo-cortical feedback loops.

Structure of a typical single trial, showing tonic and phasic power:

Not under „volitional control", change over life cycle, in response to fatigue, distress or neurological disorders, etc.

Stimulus

Tonic power
typically measured in a reference interval

Phasic power
measured in a poststimulus interval

-1500   -1000   500   0   500   1000 ms

The functional meaning of the relationship between <u>tonic</u> and <u>phasic</u> band power

-Double dissociation between Alpha and Theta -

Event (task)-related:
Increase/Decrease in bandpower as compared to reference interval.
Under „volitional control"

Phasic and tonic THETA

Standard Case

Tonic power stays at a stable level, phasic power increases

Phasic power reflects processing capacity

Best Case

Tonic power decreases, phasic power increases

Increased processing capacity

Good performance

Theta power Increase

Decrease

Tonic power

Phasic power

Tonic power

Phasic power

Working Memory (**Theta**)

Hippocampocortical feedback loops

Phasic and tonic ALPHA

Standard Case

Tonic power stays at a stable level, phasic power decreases

Best Case

Tonic power increases, phasic power decreases

Phasic power reflects processing capacity

Increased processing capacity

Alpha power Increase

Decrease

Tonic power

Phasic power

Tonic power

Phasic power

Lower Alpha presumably is working as a kind of mediator among the two „masteroscillations": Theta for WM and Upper-Alpha for LTM demands.

Sensory (semantic) Long-Term-Memory Demands (Upper-**Alpha**)

Thalamocortical feedback loops

Figure 13. Analysis of tonic and phasic (= event-related) band power changes in the alpha and theta band

The functional meaning of the interplay between tonic and phasic changes, as well as of alpha and theta oscillations is shown It is known that (tonic) alpha power is lowered and theta power is enhanced in subjects with a variety of neurological disorders (→"worst case"). Note that this double dissociation between alpha vs. theta and tonic vs. phasic changes can be observed only when fixed frequency bands are abandoned.

Steriade et al. (1990, 1999) and much earlier Andersen and Andersson (1968) provided evidence that EEG-alpha activity discussed indeed is related to thalamo-cortical oscillations with a specific role for memory processes. The basic idea concerning those feedback loops is depicted in figure 14.

Corticothalamic reentrant loops

A

Far from just representing noise, the spontaneous activity of **corticothalamic neuronal networks** <u>determines</u> how receptive the brain is to external stimulation and also how it influences the quality of perception.

Steriade, 2000 (p. 243)

...reflecting intrinsic neuronal properties for global oscillations (Steriade, 2000)

But neocortical neurons still display, periodically, epochs of enhanced excitability → **Dreaming Mentation & Memory Consolidation**

Cortical networks

Picture processing

Expecting visual stimulus → pre-activation or preparation for visual gating

Counting pictures
Memorizing
Comparing
Ignore distractors

As tasks get more difficult more cortical networks have to be activated

Feedback loops become longer and therefore oscillations slower once systems are heavily loaded

During slow-wave sleep the **brain is disconnected** from the external world **due to synaptic inhibition in the thalamus**.

→ Occurrence of high-amplitude delta activity (less than 3.5 Hz).

Thalamus

B

Pre-stimulus subbands oscillate independently from each other

At stimulus (due to alpha) they reorientate their phase and are beeing transiently „bind" together or „tuned in"

→ „Waxing & Waning"

Alpha: An „attention-manager"

Tunes or bindes transiently different subbands together. Once that is achieved, subbands are allowed to continue oscillating autonomously (and automatically).

Figure 14. Corticothalamic reentrant loops and alpha as a type of "attentional manager"

A: The interaction of thalamus and cortical networks is shown schematically. During the transition from alert wakefulness to sleep onset alpha power decreases whereas theta and delta power increase. REM sleep (with a high probability of dreaming episodes), however is characterized by a low voltage desynchronized EEG with an irregular pattern of bursts of alpha activity particularly at occipital leads. The decrease in alpha during parts of REM sleep can be interpreted in terms of an "event-related" suppression or "desynchronization" of the kind that can be observed during an alert subject performing some type of task (Klimesch, 1999). **B:** Alpha can be thought of as a kind of attentional manager, which aligns different subbands to each other in response to a stimulus, thereby achieving that different subsystems (oscillations) are adjusted to a certain task or processing mode. Once they are "tuned in" they are left on their own and continue to work "autonomously".

5 Bridging the gap between early evoked ERP components and brain oscillations

5.1 Theoretical background

The leitmotif or core hypothesis of the present work is, that event-related potentials (ERPs) might be nothing more than an ensemble of oscillations. Or as suggested by Basar (1980, cited in Basar, 1998) evoked potentials should be thought of as the superposition of several "evoked oscillations". Subsequently, I will try to bring together the so far discussed theoretical considerations concerning ERPs and brain oscillations. Ultimately, this will lead us to some specific assumptions and hypotheses, which then either will be supported or have to be rejected based on the evidence presented in the following (experimental) sections.

5.1.1 Introduction

Event-related potentials (ERPs) are an important tool to study neural correlates of sensory, attentional and other cognitive processes. In contrast to analyses in the frequency domain, ERPs reflect neural processes that are strictly time locked with respect to the presentation of a stimulus. The early components consist of sharp positive and negative peaks that form the P1-N1 complex. They appear to reflect modality specific sensory processes that are sensitive to the direction of attention and are well investigated in the visual (e.g., Eason, 1981; Hillyard & Münte, 1984; Mangun & Hillyard, 1990; Luck, Fan, & Hillyard, 1993; Hillyard, Luck, & Mangun, 1994) and auditory information processing domain (e.g., Hansen & Hillyard, 1980; Woldorff, Hansen, & Hillyard, 1987; Woldorff & Hillyard, 1991; Wood & Cowan, 1995a,b), as discussed earlier on.

The fact that these early components are sharp waves with alternating polarities clearly demonstrate that neural synchrony occurs in narrow time windows probably alternating between inhibitory and excitatory processes (reflected by the P1 and N1 component respectively; Hillyard, Luck & Mangun, 1994, p. 23). This, however, is exactly the way an oscillatory process is operating. As was shown e.g., by Bland et al. (1995) and Buzsaki et al. (1994), variations in the strength of the local field potential are related to periods of enhanced or attenuated multi-unit activity (which reflects bursts of action potentials).

Another interesting point is that the interpeak latency of these early peaks (e.g., at posterior sites during visual stimulation: P1 at 90-120 ms and N2 at 150-190 ms; cf. Hillyard, Luck & Mangun, 1994) is about 65 ms which corresponds to a period of 130 ms (a half period is the latency between peaks of different polarity) and, thus, to a frequency of about 7.7 Hz (see also

subsequent sections presenting experimental evidence and further exemplary data from classical P1-N1 literature).

Numerous studies indicate that the P1-N1 complex reflects sensory and early attentional processes. A very similar interpretation holds true for the alpha rhythm. Since the work of Berger, alpha was thought to reflect visual and attentional processes. However, more recent studies suggest, that only the lower alpha band of about 6-10 Hz is related to attention and that alpha is not restricted to occipital areas but by using MEG instead of EEG can also be observed in the auditory cortex (Tihonen et al. 1991, cited in Hari, 1999). Thus, each sensory area seems to have its own alpha like rhythm as well as its own P1-N1 complex.

The anterior N1 has a shorter latency (of about 100 -140 ms) than the posterior N1 and appears to have a frequency characteristic in the theta band (cf. Hillyard, Luck & Mangun, 1994; fig.6-7). There seems to be an interplay between alpha (reflected by the P1-N1 complex) and theta (plugging in at the N1-component).

Additionally, there is a relationship between the time course of alpha desynchronization and the appearance of the P1-N1 complex. In many cases – depending on the task, recording site and the exact frequency limits of the lower alpha band – alpha (at least in the lower band of about 6-10 Hz) synchronizes during the time window of the P1-N1 complex and starts to desynchronize only after the P1-N1 complex has disappeared (as was schematically shown in fig.2). A possible explanation for this phenomenon would be, that relevant cortical areas are "tuned" for processing or task- demands by means of the alpha-system, which subserves some kind of "managing"-function. Once that is achieved, the attention-managing function is not longer needed - the relevant cortical areas continue to work on their own – and, thus the alpha-system looses phase-locking and fades away. Typically this event-related alpha desynchronization is observed about 300 ms post-stimulus.

5.1.2   Demonstrated relationships between spontaneous EEG and ERPs

In the recent years there has been increasing interest in the relationship between spontaneous EEG activity and a number of ERP components. This young but expanding area of study follows predominantly the pioneering work of Erol Basar and colleagues. Our research group similarly sees the EEG as arising from the activity of an ensemble of neuronal generators producing rhythmic activities in several frequency ranges. These generators are usually randomly active, but when stimulated they become coupled and act together in a coherent manner. The superimposition of such coherent activity (in particular frequency

ranges) is suggested to -at least partly- determine the ERP components, as discussed earlier (see fig. 6).

According to Basar (1997) amplitude, time course, and frequency content of evoked potentials (N100-P200 complexes) strongly depend on the amplitude of alpha activity prior to a sensory stimulation and Brandt (1997) showed that the generation of spontaneous EEG can produce visual-evoked-potential like wave forms when triggered by pulse-like signals. Furthermore, Basar and colleagues demonstrated the substantial influence of pre-stimulus alpha-amplitude and phase angle on the visual and auditory N1-component. This model provides support that the spontaneous-ongoing 10-Hz activity and the VEPs are presumably generated by some of the same neural structures, and rather due to a distributed "pacemaker-system" than dipolar sources.

Whereas Basar's group has long reported an inverse relationship between pre-stimulus alpha activity and ERP amplitudes (e.g., Basar, 1980, 1989, cited in Basar, 1998), contradictory results have been constantly reported by Brandt's group (e.g., Brandt, 1997). Basar et al. showed that high amplitude 10-Hz activity preceding the stimulation reduced the amplitudes of evoked potentials by 30% (Basar et al., 1997) and implicated that therefore 10-Hz activity cannot be considered just as noise to be eliminated from evoked potential recordings but in this case the EPs would contain alpha coding.

Brandt, on the other hand, reported greater pre-stimulus alpha amplitude resulting in larger ERP amplitudes. The reason for this discrepancy remains to be resolved, but might be attributed to filter-artifacts as noted by Brandt (1997).

Barry et al. (2000) also find higher levels of pre-stimulus alpha activity resulting in larger ERP components (in an auditory oddball paradigm). Especially their N1-P2 (peak-to-peak amplitude) results at Pz support the findings of Brandt's group. Barry et al. conclude from their data that pre-stimulus alpha activity directly contributes to the amplitudes of the major ERP components (in the target stimuli in an auditory oddball paradigm) and also ascribe the effect to a strong "phase realignment" of alpha activity.

According to Polich (1997) a positive relationship between pre-stimulus EEG spectral power, primarily in the theta and alpha bands and the amplitude of the P300 component has already long been demonstrated (e.g., Jasiukaitis et al., 1990; Basar et al., 1989, as cited in Polich, 1997). Polich (1997), as well found individual variation in background EEG activity associated with P300 amplitude and latency variability. Doppelmayr et al. (1998), however report that the prestimulus (reference) level of absolute alpha band power is related to a strong degree of alpha suppression as measured by ERD and that the opposite holds true for the theta

band, where a low level of band power during the reference interval is related to a pronounced increase in band power during the processing of the target stimulus. This evidence suggests that high alpha power is related to decreased ERP-components as reported by Basar et al (1998). Presumably the contradictory results are due to different ERP-components these studies focused on. For example, there is evidence that the P300 is readily modified by the prestimulus levels of theta activity, whereas little is known about the earlier components (P1, N1), which might behave completely different as suggested by results from Doppelmayr et. al (1998). However the question remains, if this event-related alpha desynchronization also possibly affects as early components as the P1 (or N1). Other alternative explanations for these contradictory results will be discussed later on (refer to section 6.4.2).

5.1.3   Consequences and general assumptions

If the P1-N1 complex is indeed the manifestation of an oscillatory process (in the alpha and/or theta frequency range) these components must be considered not only time locked but also phase locked with respect to the appearance of a stimulus. Because brain oscillations occur rather continuous in time it would be wrong to assume that a rhythm appears or disappears in response to the presentation of a stimulus or any other event. Instead it is assumed that oscillations are modulated by events (cf., fig. 6).

In the case of the P1-N1 complex, it is assumed that ongoing oscillations are modulated in a way that e.g., the presentation of a stimulus leads to a sudden but transient phase locking of these oscillations. The P1-component for example, is postulated to be equivalent to phase-locked alpha activity, which aligns (reorganizes) itself in response to a stimulus. The important consequence of this assumption is that the oscillations will already be there long before a stimulus is presented and thus can be measured already during a prestimulus period. Band power measures which just reflect the strength of an ongoing rhythm regardless of any phase relationship reveal an increase during a prestimulus period of about 250 ms. This finding indicates that due to the anticipation an ongoing oscillation increases its amplitude already before the stimulus is presented and becomes phase locked to the stimulus, once it is presented.

The subsequent experimental chapters comprise a recognition task with visual stimuli realized in our own laboratory, as well as a selection of some visual (spatial) attention tasks (utilizing ERPs) obtained from the literature. Taken the assumptions that every EP contains oscillatory responses in various frequency ranges depending on the task or cognitive demands (Basar, 1998) and the fact "that the amount of EEG-power in the theta and alpha frequency

range is indeed related to cognitive and memory performance in particular" (Klimesch, 1999, p. 189) suggest that the ERPs discussed subsequently should reflect predominantly oscillatory responses in the alpha and/or theta range.

Specific networks are thought to superimpose on more general neuronal systems, as those serving general attentional demands (lower-alpha activity).

- Lower-alpha activity should be varying with respect to attentional demands. For example, in the visual recognition task topographical effects are expected, in the way that with a shift of the attentional focus (visual encoding and retrieval) different brain structures are "favored" and this should show up as a (somehow) "lower-alpha modified" ERP.

- Upper alpha-activity should be dominant for (sensory-) semantic long-term memory demands (search and retrieval), but might be difficult to discriminate from the residual (lower) alpha system.

- "Theta oscillations" should come forward predominantly for working memory demands (e.g., visual encoding). Therefore, a shift to slower oscillations is expected for encoding, most likely over structures well known for visual encoding (occipital).

5.1.4 Hypotheses

This will be discussed mainly on the basis of three "measures":

a) Absolute time of appearance (for the early ERP-components; P1, N1, P2)

b) Peak-to-peak power and latencies (for P1, N1, P2 – peaks)

c) Standard ERPs (broad-band filtered) vs. filtered ERPs (e.g., Alpha-ERPs)

discussed on the basis of descriptive, as well as correlational data.

If the P1-component indeed is – as postulated - equivalent to phase-locked alpha activity, this early ERP-component is strongly expected to vary systematically with IAF (Hz) and/or IAF-power. Furthermore filtered alpha-ERPs should be able to (almost) completely account for the respective component (P1 and/or N1) in the standard ERP.

Specifically, alpha activity known as the most dominant oscillation in human EEG might be able to "relocate" early ERP components in the way, that higher IAF (individual alpha frequency) is accompanied by an earlier appearance of P1, N1 and/or P2-components.

Alpha frequency is also known to be an indicator for the speed of cognitive and memory performance and good performers are known to retrieve information faster from memory.

The behavioral data which is available for the visual recognition task, allows to take a closer look at the relationship between memory performance and ERPs. For example, it is assumed that the commonly speeded responses from good (memory) performers will be accompanied by earlier ERP-components (e.g., P1 and/or N1).

And in connection with alpha-activity (IAF) it would be terrific if a significant relationship between those three could be demonstrated. That would mean, higher IAF correlated with better memory performance – which already has been demonstrated by Klimesch (1996) - and earlier appearing ERP-components.

If indeed oscillatory activities and phase-locking of ongoing EEG is the "primary generator" for ERPs, peak-to-peak latencies (P1-N1; N1-P2) should lie within the alpha and/or theta range depending on information-processing demands. In particular encoding of pictures should move those early components further apart as an underlying theta oscillation is expected, as well as closer components should result from an underlain (upper-) alpha oscillation prevailing for search and retrieval processes.

Usually visual encoding would be expected predominantly in occipital cortical regions (surrounding the primary visual cortex), whereas recognition or retrieval is classically reported to be dominant over parietal sites.

As it is assumed that respective neuronal networks synchronize within the first 300 ms (encompassing the P1-N1 complex) higher peak-to-peak amplitudes (due to increased phase-locking) in the event-related potentials are expected (as depicted in fig. 6) for e.g., attended (as compared to unattended) locations in visual spatial attention tasks. Additionally, in the visual recognition task topographical effects are expected, in the way that with shifting the locus of the attentional focus different brain structures should be predominantly "favored". Or more exactly, higher (peak-to-peak) component-amplitudes are expected over occipital sites for visual encoding, whereas the attentional "benefits" should show up at parietal sites for (visual) retrieval.

With regards to the relationship between individual alpha-power and ERPs making an assumptions is tricky. The results reported in the literature are contradictionary (as reported earlier) and these studies all refer to pre-stimulus alpha activity, whereas the present study refers to the power of the individual alpha peaks (during relaxed recordings preceding the experiment). However if maintaining the logic presented much earlier (fig. 6) alpha power

decrease might occur with stimulus-presentation, but is usually seen as event-related desynchronization much later (around 300 ms post-stimulus) due to the contrary effect of phase-locking. Thus, it might be assumed that in accordance with Basar et al. (1998) and Doppelmayr et al. (1998) this early components (P1, N1) – which are thought to be heavily influenced by alpha activity – possibly decrease in amplitude, for high resting IAF-power.

6   Experimental evidence: "Snodgrass study"

6.1   Introduction

Evidence is presented that early evoked ERP components (generated by the P1-N1 complex), which have been shown to reflect sensory and early attentional processes have a frequency characteristic that lies within the theta and/or alpha frequency ranges. Subsequently no components earlier then the P1 will be considered, as it has been shown, for example, in the visual domain that attentional modulation does not occur before reaching extrastriate cortex.

Components like the C1 in the primary visual area (striate cortex) seem to be widely attention independent and information there is rather "automatically" processed, therefore it is unlikely that there the oscillatory activity I focus on (alpha, theta) should play a significant role. Rather the close relationship between "information processing modes" and the frequency decomposition of ERPs during encoding and retrieval will be of main interest.
Most importantly, the alternative ERP-model - stating that event-related potentials (ERPs) happen to be oscillatory manifestations - presented earlier will become further support.

Wouldn't it be intriguing if it could be shown that those early ERP components happen to appear earlier as a function of individual alpha frequency (IAF)? If that is the case, and e.g., the P1-component appears earlier for "high IAFs", this would strongly suggest that the P1 might be above all phase-locked 10 Hz or alpha activity.
Similar approaches and views are still rare but are becoming more and more common. For example, Robinson (1999) (using a simple auditory oddball) suggests that the P1 and P2 peaks in the unfiltered ERP relate mainly to the 10 and 4 Hz frequency responses, whereas the N1 peak seems to be a composite of overlapping 4 and 7 Hz deflections.

6.2   Material and Methods

6.2.1   Participants

After informed consent, a sample of 45 right-handed subjects participated voluntarily in the experiment. 34 subjects (25 females, 9 males) for the encoding and 35 (25 females, 10 males) subjects for the retrieval condition finally remained for data analysis. The mean age was 23.1 years with a range of 17 to 32 years.

6.2.2 Design and Material

A set of 70 target pictures taken from Snodgrass and Vanderwart (1980) was presented during the study session. In order to eliminate primacy and recency effects the first and last five pictures were eliminated for data analysis, thus 60 pictures remained as targets.

After about 6 min, subjects made a recognition judgment for each of 180 pictures, 120 being distractors and 60 being the targets (all from: Snodgrass & Vanderwart, 1980) by verbally responding "yes" or "no". Pictures were presented on a computer monitor and a trial consisted of a 2 sec (0-2000 ms) blank interval, the presentation of a picture for 1 sec (2000-3000 ms) and another blank interval of 4 sec in the study and 5 sec in the recognition session.

6.2.3 Apparatus and EEG Recording

EEG-signals were amplified by a 32-channel biosignal amplifier system (frequency response: 0.16 to 30 Hz), subjected to an anti-aliasing filterbank (cut-off frequency: 30 Hz, 110 dB/octave) and were then converted to a digital format via a 32-channel A/D converter. Sampling rate was 128 Hz. During data acquisition, EEG signals were displayed online on a high resolution monitor and stored on disk.

A set of 25 silver electrodes was placed according to the International Electrode (10-20) Placement-system, at F3, F4, Fz, FC1, FC2, FC5, FC6, C3, C4, Cz, T3, T4, CP1, CP2, CP5, CP6, P3, P4, Pz, PO1, PO2, PO3, PO4, O1 and O2. In addition, two earlobe electrodes were attached to the left and right ear. Data were recorded against a common reference placed on the nose and off-line algebraically re-referenced to linked earlobes. The electrooculogram (EOG) was recorded from 2 pairs of leads in order to register horizontal and vertical eye movements. All of the epochs in each task were carefully checked individually for artifacts (eye blinks, horizontal and vertical eye movements, muscle artifacts etc.) by visual inspection.

6.2.4 Procedure

After rejecting artifacts and erroneous trials, an average of 37 epochs remained for correctly identified targets in the encoding condition (range: 20-50) and 43 for the retrieval condition (range: 30-56). Epochs were categorized with respect to (later) correctly identified targets ("Hits") for the retrieval just as for the study phase. All analyses were carried out for "Hits" (correct recognition) only. In the residual sample (comprised of 35 Ss for retrieval and 34 subjects for the encoding condition) an average of 46 pictures was being correctly recognized.

For analyzing evoked alpha and theta responses, individually filtered ERPs were calculated in addition to the standard ERPs (0.5 to 30 Hz). Because it was shown repeatedly that the use of fixed frequency bands leads to distorted results frequency bands were defined individually by using individual alpha frequency IAF(i) as cut off point, for subbands of 2 Hz each (see Klimesch, 1999). We distinguish between an upper alpha band (falling 2 Hz above IAF(i)), two lower alpha bands (termed lower-1 and lower-2 alpha), and a theta band (falling below IAF(i) in steps of 2 Hz). Furthermore, a broad alpha ERP was calculated falling 4 Hz below IAF(i) and 2 Hz above IAF (i). The filtered ERPs are obtained by averaging the band pass filtered data over the number of good trials.

Averaged over the sample of subjects, alpha frequency was 10.04 Hz (9.99 Hz for encoding), the standard deviation being 1.00 Hz. IAF-Power was obtained by calculating the mean of IAF(i) ± 0,5 Hz (eyes closed condition at rest) collapsed over Fz, Pz, P3, P4, PO3, PO4, O1 and O2. Furthermore, local IAF-Powers were computed for each of the respective sites (IAF-Fz, IAF-Pz, etc.) using the same logic .

ERPs (scaled 0 to 450ms) were first manually inspected for early ERP peaks (P1, N1, P2, N2; termed after sequential order) on a 22inch high-resolution monitor at electrode sites Fz, Pz, O1 and O2. As individually varying time windows for each component were allowed, the absence of e.g., an early P1 lead to respectively later subsequent components. Therefore varying time windows were abandoned, and replaced by fixed ones; Furthermore the unstable nature in time and reflection of the main purpose of the study led to drop the N2-component. On the other hand the promising results of the first rating, urged to add several electrode sites (cf., Appendix, Figure A1.) for further data analysis (P3, P4, PO3, PO4). Referring to P1/N1 literature in the visual domain (e.g., Luck, Fan, & Hillyard, 1993; Hillyard, Luck, & Mangun, 1994; Clark, Fan, & Hillyard, 1995) and as a result of the knowledge we obtained from the previous rating, we set fixed time windows as follows:

> P1-component: 40 – 140 msec
> N1-component: 95 – 205 msec
> P2-component: 140 – 290 msec

Together with introducing the fixed time windows we also tightened the rules concerning the rating of ERP-components. We decided that within the respective time windows the highest peak has to be judged as P1, N1 or P2. By applying this strict rule, though sometimes being counterintuitive, we met the objection of biasing due to selective data-acquisition. Again the data was first rated manually (ERPs scaled 50-350 ms), but then a "house-made" computer-aided "Peak-Detection Program" was utilized for determining automatically peaks

in user-defined time-windows. Computerized peak-rating was monitored online and checked for validity using the manually obtained data.

Group-averages were calculated for "low" (< 9.75 Hz), "medium " ($9.75 – 10.25$ Hz) and "high" (> 10.25 Hz) IAF participants. Another subsample was computed for "high" (> 50 "hits") and "low" (< 40 "hits") "recognizers". All the computations were performed separately on the "encoding" and the "retrieval" condition.

Last, but not least in addition to absolute latencies and component amplitudes, peak-to-peak latencies and peak-to-peak amplitudes were calculated for P1-N1, N1-P2 and P1-to-P2 components. Note that peak-to-peak latencies are specified as frequencies and are calculated on behalf of a full period (e.g., 50 ms P1-N1 peak-to-peak latency correspond to 100 ms of a full period or 10 Hz). Bivariate one-tailed correlations were calculated for each component in the two experimental conditions (encoding and retrieval) with an alpha level set at .05 for all statistics.

6.3   Results

	Mean	SD	N
IAF (Hz)	10,04	1,00	35
IAF-Ampl. (µV)	11,31	12,31	34
Age	23,06	3,70	35
Recognized	46,11	6,57	35

Table 1. General Descriptives

Means and standard deviations (SD) are shown for IAF (Hz), IAF-amplitude (µV), age and correctly recognized items ("Hits"). (One value is missing for IAF-amplitude, due to corrupt data.)

According to Klimesch (1996), 95% of all participants are expected to have an alpha frequency lying within a range of 8 to 12 Hz. Koepruner et al. (1984) even postulates a linear relationship (alpha peak frequency = 11.95 – 0.053 x age) within the age range of adult participants. Considering this formula, a peak around 10.7 Hz for an average of 23 year old participants was expected; approximately the age of students used as participants in the present study. In the present study the mean individual alpha peak was found to be 10.04 Hz ($\underline{SD} = 1.0$), with the mean amplitude being 11.3µV.

6.3.1   Descriptives (absolute data)

Figures 15-17 show the mean latencies and mean amplitudes (group-average) for the three ERP-components P1, N1 and P2 for both conditions (encoding and retrieval). For a complete listing of the respective data refer to table A5. Generally speaking component latencies

increase from anterior to posterior sites. For retrieval earlier P1-components can be observed at parietal sites (Pz, P3, P4), whereas N1 components appear earlier during encoding at parietooccipital (PO3, PO4) and occipital (O1, O2) electrode sites. P1-amplitudes are enhanced during encoding compared to retrieval at parietal (Pz, P3, P4) and parietooccipital sites (PO3). N1 amplitudes are enhanced for all inspected sites (Fz, Pz, P3, P4, PO3, PO4, O1, O2) during retrieval, whereas P2-amplitudes are enhanced for the encoding condition all over.
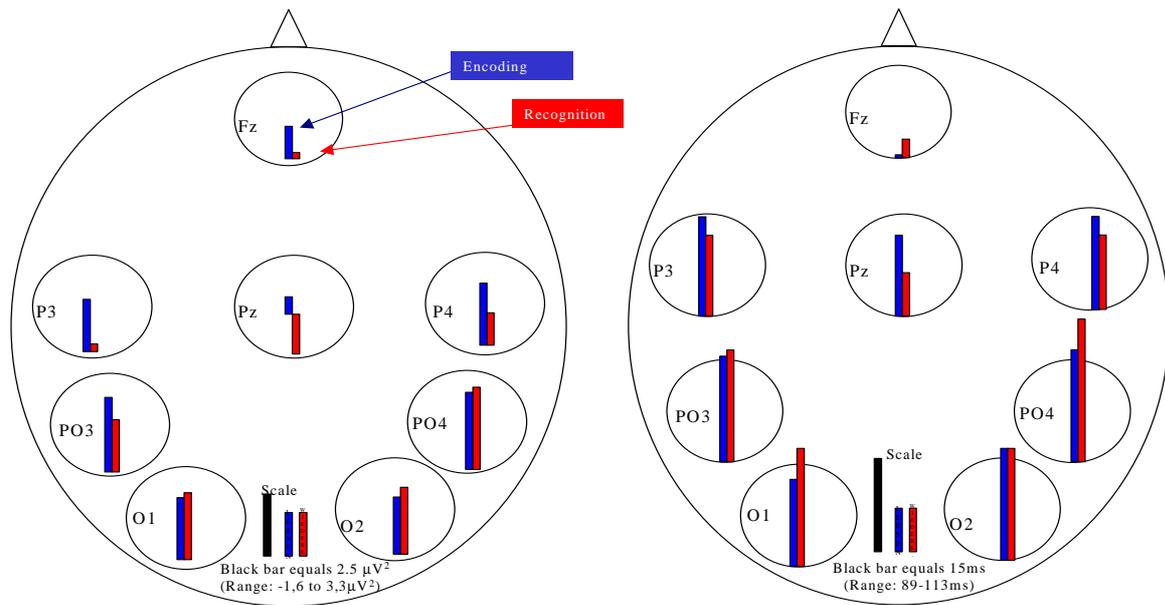
Figure 15. P1- amplitudes and latencies

Mean amplitudes of the P1-component (left) and mean P1-latencies (right) for the encoding (blue bars) and retrieval (red bars) condition are shown for the respective electrode sites (Fz, Pz, P3, P4, PO3, PO4, O1 and O2). The bar-lengths correspond to the amplitudes (black bar equals $2.5\mu V^2$) and latencies (black bar equals 15ms) of the P1-component at the respective sites. P1-amplitudes vary between –1.6 to $3.3\mu V^2$ (i.e., smallest red bar at Pz and highest at PO4) and P1-latencies range from 89 to 113ms (i.e., earliest P1 at Fz, latest at PO4). Note that for retrieval earlier P1-components can be observed at parietal sites (Pz, P3, P4), whereas P1-amplitudes are enhanced during encoding compared to retrieval at parietal (Pz. P3, P4) and parietooccipital sites (PO3).
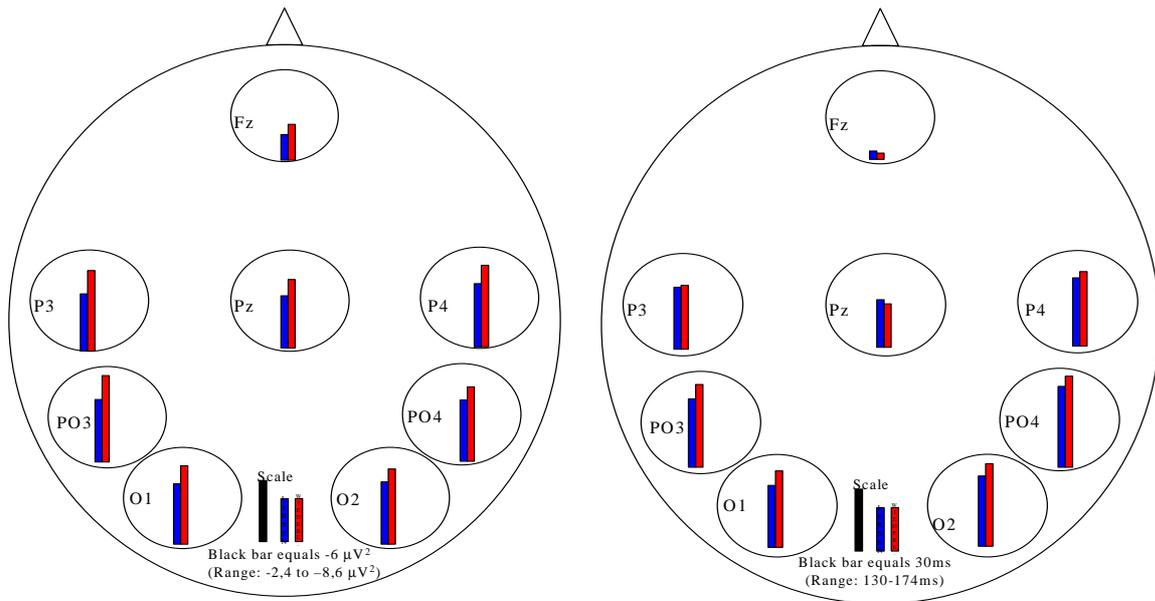
Figure 16. N1- amplitudes and latencies

Mean amplitudes of the N1-component (left) and mean N1-latencies (right) for the encoding (blue bars) and retrieval (red bars) condition are shown. N1-amplitudes vary between –8.6 to –2.4μV^2 (Note that negative is up; black bar equals -6μV^2) and N1-latencies between 130 and 174ms (black bar equals 30ms). Note that N1 components appear earlier during encoding at parietooccipital (PO3, PO4) and occipital (O1, O2) electrode sites, whereas N1 amplitudes are enhanced for all inspected sites (Fz, Pz, P3, P4, PO3, PO4, O1, O2) during retrieval.
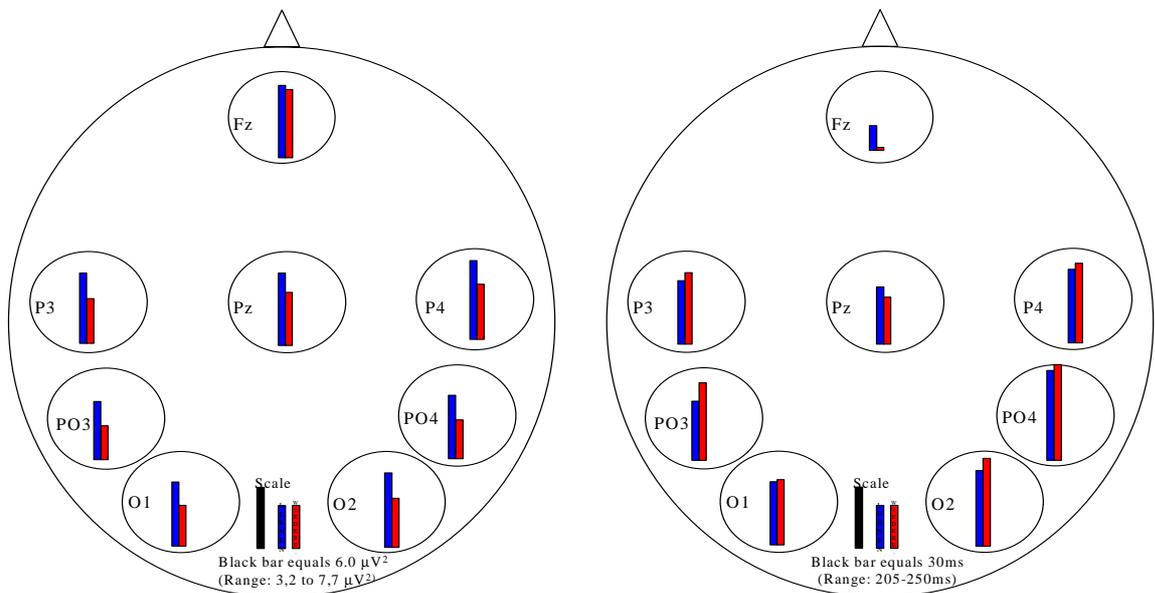
Figure 17. P2- amplitudes and latencies

Mean amplitudes of the P2-component (left) and mean P2-latencies (right) for the encoding (blue bars) and retrieval (red bars) condition are shown. P2-amplitudes vary between 3.2 and 7.7μV^2 (black bar equals 6μV^2) and P2-latencies range from 205 to 250ms (black bar equals 30ms). Note that P2-amplitudes are enhanced for the encoding condition all over.

6.3.2   Descriptives: Peak-to-Peak Latencies and Amplitudes

In the next table (table 2) the **<u>peak-to-peak latencies</u>** of the P1-, N1-, and P2- component

are interpreted as a half period of an oscillation, therefore the values in the table stand for the

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respective frequencies (e.g., half period 50 ms for P1-to-N1 → full period 100 ms or 10 Hz). A table for all electrode sites can be found in the Appendix (table A6).

P1-to-N1 peak-latencies are substantially shorter or in other words correspond to higher frequencies ($\underline{M}$ = 10.36 Hz, $\underline{SD}$ = 4.13) as compared to N1-to-P2 peak-to-peak latencies ($\underline{M}$ = 7.36 Hz, $\underline{SD}$ = 2.48).

	Mean	SD	N		Mean	SD	N
	ENCODING				RETRIEVAL		
P3 P1-N1	10,259	3,51	33	P3 P1-N1	10,694	6,12	32
P3 P1-P2	7,904	1,62	33	P3 P1-P2	7,883	2,31	32
P3 N1-P2	7,084	2,17	34	P3 N1-P2	7,375	2,72	32
PZ P1-N1	10,867	3,94	30	PZ P1-N1	11,079	6,03	31
PZ P1-P2	7,922	1,43	30	PZ P1-P2	8,416	3,22	31
PZ N1-P2	7,085	2,63	34	PZ N1-P2	7,881	3,41	33
O1 P1-N1	10,043	3,76	32	O1 P1-N1	10,053	4,02	31
O1 P1-P2	7,938	1,64	32	O1 P1-P2	8,196	1,94	31
O1 N1-P2	6,905	1,54	34	O1 N1-P2	7,912	2,32	33
O2 P1-N1	9,786	3,13	33	O2 P1-N1	8,751	2,87	33
O2 P1-P2	7,699	1,35	33	O2 P1-P2	7,394	1,54	33
O2 N1-P2	6,804	1,83	34	O2 N1-P2	7,063	2,17	33
Mean / Standard deviation (all)	P1-to-N1	10,40	3,81	P1-to-N1	10,33	4,44	
	N1-to-P2	7,07	2,23	N1-to-P2	7,65	2,73	

Table 2. Peak-to-Peak latencies (in frequencies)

Looking at **peak-to-peak amplitudes** (table 3) higher N1-to-P2 interpeak-amplitudes can be observed during encoding for all sites except lead Fz. P1-to-N1 peak-to-peak amplitudes on the other hand are throughout higher for retrieval as compared to encoding at all sites except Fz and Pz. For example, P1-to-N1 amplitudes (retrieval) at PO3 ($\underline{M}$ = 10.60, $\underline{SD}$ = 5.59) and PO4 ($\underline{M}$ = 10.69, $\underline{SD}$ = 5.80) were higher as compared to $\underline{M}$ = 9.08 ($\underline{SD}$ = 4.61) and $\underline{M}$ = 8.72 ($\underline{SD}$ = 4.98) for encoding, as well as N1-to-P2 during encoding at O1 ($\underline{M}$ = 12.34, $\underline{SD}$ = 5.32) and O2 ($\underline{M}$ = 13.50, $\underline{SD}$ = 6.50) were higher as compared to retrieval ($\underline{M}$ = 11.81, $\underline{SD}$ = 6.49; $\underline{M}$ = 12.31, $\underline{SD}$ = 6.81).

	Mean	SD	N		Mean	SD	N
	ENCODING				RETRIEVAL		
P3 P1-N1	8,03	4,49	33	P3 P1-N1	8,25	5,16	34
P3 N1-P2	12,68	5,59	34	P3 N1-P2	12,42	6,64	34
P4 P1-N1	8,50	4,61	32	P4 P1-N1	9,79	5,67	33
P4 N1-P2	14,04	6,10	34	P4 N1-P2	13,41	6,45	33
O1 P1-N1	8,44	4,98	32	O1 P1-N1	10,71	6,25	33
O1 N1-P2	12,34	5,32	34	O1 N1-P2	11,81	6,49	35
O2 P1-N1	8,28	4,36	33	O2 P1-N1	10,22	5,55	35
O2 N1-P2	13,50	6,50	34	O2 N1-P2	12,31	6,81	35
Mean / Standard	P1-to-N1	8,20	4,49	P1-to-N1	9,42	5,30	

Table 3. Peak-to-Peak amplitudes

6.3.3 Main findings (correlational relationships)

Bivariate correlations (1-tailed) were run and revealed several significant effects. An alpha level of .05 was used for all statistical tests. Refer to table 4 for an intercorrelation matrix depicting the most important findings. Furthermore a more complete matrix is available in the Appendix (table A1-A3).

With an alpha level of .05, the **individual alpha frequency (IAF)** correlated significantly with P1-**latencies** for the encoding, as well as for the retrieval condition (for a schematic representation refer to fig. 18). For the encoding condition IAF was positively correlated with the latency of the P1 component at electrode site O2, r (33) = -.296, p < .047, and nearly significant at site PO4, r (30) = -.294, p = .057. For the retrieval condition correlations significant at the 0.05 level (1-tailed) were found for electrode sites Pz (r (33) = -.352, p = .022), PO4 (r (34) = -.326, p = .03), O1 (r (33) = -.311, p = .039) and O2, r (35) = -.371, p = .014.
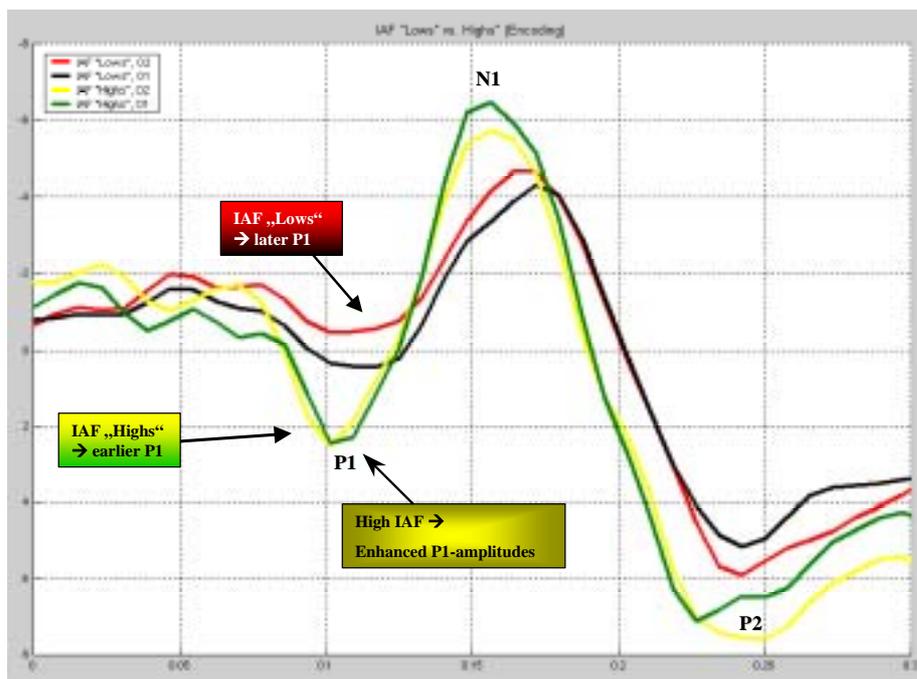
Figure 18. Schematic representation of the relationship between IAF and early ERP components
Shown is the subsample of IAF "Highs" vs. IAF "Lows" during the encoding condition.

IAF further correlated significantly with the **amplitude** of P1 and P2 components in both tasks (refer to fig. 20-21 and/or fig. A3-A4). For the P1-component during encoding significant correlations could be found with site PO3 (r (33) = .295, p = .048), O1 (r (32) = .351, p = .024) and O2 (r (33) = .306, p = .042). For retrieval electrode sites PO3 (r (35) = .327, p = .028) and O1 (r (33) = .331, p = .03) were statistically significant, whereas the

correlation with the P1-component at O2 was nearly significant, $\underline{r}$ (35) = .274, $\underline{p}$ = .055. For the P2-component a significant relationship could only be found for lead PO4. Individual alpha frequency correlated positively with P2-amplitudes at PO4 during encoding, $\underline{r}$ (33) = .332, $\underline{p}$ = .03, and nearly significant for retrieval, $\underline{r}$ (31) = .288, $\underline{p}$ = .058.

IAF-power revealed several significant correlational relationships with P1-latencies and amplitudes, as well as with N1-latencies. IAF-power correlated highly significant with later P1-appearance at PO4, $\underline{r}$ (30) = .495, $\underline{p}$ = .003 and significant at the 0.05 level at electrode site O2, $\underline{r}$ (33) = .305, $\underline{p}$ = .042 for the encoding condition, as well as (highly) significant with P1-latencies at leads PO3 ($\underline{r}$ (34) = .313, $\underline{p}$ = .036) and PO4 ($\underline{r}$ (33) = .412, $\underline{p}$ = .009) during retrieval. The P1-component decreases in amplitude with higher IAF-power at several sites for both conditions. P1 amplitudes at sites P3 ($\underline{r}$ (32) = -.299, $\underline{p}$ = .048) and O2 ($\underline{r}$ (33) = -.332, $\underline{p}$ = .030) during encoding and Pz ($\underline{r}$ (32) = -.375, $\underline{p}$ = .017), P3 ($\underline{r}$ (34) = -.380, $\underline{p}$ = .013), O1 ($\underline{r}$ (32) = -.335, $\underline{p}$ = .031) and O2 ($\underline{r}$ (34) = -.293, $\underline{p}$ = .046) during retrieval all show negatively significant correlations with IAF-power. The N1-component shows a highly significant correlation with IAF-power at site PO4 ($\underline{r}$ (32) = .416, $\underline{p}$ = .009) and a significant one at O2 ($\underline{r}$ (33) = .346, $\underline{p}$ = .024) for N1-latencies during encoding.
Correlations of IAF-power with amplitude and latency of the P2 component during retrieval, showed clear trends towards earlier P2-components at Fz ($\underline{r}$ (33) = -.27, $\underline{p}$ = .064) and higher P2-components at O1, $\underline{r}$ (34) = .282, $\underline{p}$ = .053.

Generally speaking, correlations between **local IAF-Power** and respective component amplitudes and latencies revealed the same relationships, that is later ERP-components and decreased component amplitudes with higher (local) IAF-Power, with two remarkable deviations, though. Frontally (Fz) local IAF-power is positively correlated with P1- and P2-amplitude for the encoding condition. Furthermore the P2-component comes earlier at PO4 the higher the local IAF-power at PO4 (encoding) and occipital P2-amplitudes increase with the respective (local) IAF-power in both conditions (refer to table A1-A4 for respective statistical values).

For ERP-components P1 and N1 the number of **recognized** items correlated significantly with earlier peaks at parietal and occipital sites. In particular, for encoding P1-components correlated significantly negatively with the number of recognized items on the 0.05 level at PO4 ($\underline{r}$ (30) = -.327, $\underline{p}$ = .039) and O2 ($\underline{r}$ (33) = -.364, $\underline{p}$ = .019), and respectively for retrieval at Pz ($\underline{r}$ (33) = -.296, $\underline{p}$ = .047) and P4 ($\underline{r}$ (34) = -.325, $\underline{p}$ = .03), as well as PO4 ($\underline{r}$ (34) = -.404,

p = .009), and O2 ($\underline{r}$ (35) = -.420, $\underline{p}$ = .006) on the 0.01 level. The N1-peak appears earlier at lead P4, the more items are recognized, $\underline{r}$ (34) = -.316, $\underline{p}$ = .034 (for encoding) and $\underline{r}$ (34) = -.301, $\underline{p}$ = .042 (for retrieval). The number of correctly recognized pictures also revealed (highly) significant effects for P1-amplitudes at Pz ($\underline{r}$ (30) = -.415, $\underline{p}$ = .011) for encoding and Fz ($\underline{r}$ (35) = -.409, $\underline{p}$ = .007) for retrieval (that means smaller P1-amplitudes the more items recognized). For the P2-component (encoding condition) on the other hand, contrary correlations reached significance level. That means, that higher recognition was correlated with enhanced P2-amplitudes at PO3 ($\underline{r}$ (34) = .295, $\underline{p}$ = .045) and later P2-components at electrode site Pz ($\underline{r}$ (34) = .300, $\underline{p}$ = .042). The relationship with P2-amplitude at O1 nearly reached 0.05 significance level ($\underline{r}$ (34) = .269, $\underline{p}$ = .062). Note that IAF (Hz) was also significantly correlated with recognition, $\underline{r}$ (34) = .311, $\underline{p}$ = .037.

Peak-to-peak correlations for P1-to-N1 and N1-to-P2 amplitudes and peak-appearances (latencies) were run and revealed several significant effects, though only the most important ones will be discussed here (for a complete overview see Appendix table A7-A10). The number of recognized items correlated significantly with N1-to-P2 "latencies", meaning that the peak-to-peak distance in time increased with recognition performance during the encoding condition. The correlations were significant at electrode site Pz ($\underline{r}$ (34) = -.288, $\underline{p}$ = .049), P3 ($\underline{r}$ (34) = -.408, $\underline{p}$ = .008), P4 ($\underline{r}$ (34) = -.320, $\underline{p}$ = .033) and PO3, $\underline{r}$ (34) = -.386, $\underline{p}$ = .012.

Independent from the IAF (frequency and power) we found several significant relationships between ERP-**component latencies with the respective component amplitude**. For the P1 and N1 component this relationship (that is, later components having higher amplitudes) could only be found for Pz, whereas for the P2-component the same correlational relationship could be found for most of the parietooccipital, which was especially true for the retrieval condition (refer to Tables A1-A3 for particular values).

Encoding									
P1	**IAFHz**	**Recog**	**IAFPow**	**N1**	**Recog**	**IAFPow**	**P2**	**IAFHz**	**Recog**
Recog	.311			L-P4	-.316		L-Pz		.300
L-PO4	(-.294)	-.327	.495*	L-PO4		.416*	A-PO3		.295
L-O2	-.296	-.364	.305	L-O2		.346	A-PO4	.332	
A-Pz		-.415		A-PO3		(-.263)	A-O1		(.269)
A-P3			-.299						
A-PO3	.295								
A-O1	.351		(-.294)						
A-O2	.306		-.332						
Retrieval									
P1	**IAFHz**	**Recog**	**IAFPow**	**N1**	**Recog**				
L-Pz	-.352	-.296		L-P4	-.301				
L-P4		-.325							
L-PO3			.313						
L-PO4	-.326	-.404*	.412*						
L-O1	-.311								
L-O2	-.371	-.420*							
A-Fz		-.409*							
A-Pz			-.375						
A-P3			-.380						
A-PO3	.327								
A-O1	.331		-.335						
A-O2	(.274)		-.293						
Correlation is significant at the 0.05 level (1-tailed)									
*. Correlation is significant at the 0.01 level (1-tailed)									
( ) Nearly significant (.050-.065)									

Table 4. Intercorrelation-matrix (main-effects)

Although it has to be mentioned that the results reported here are merely of correlational nature and, thus say little about possible causal relationships. Future studies are needed to show more clearly the underlying reasons how and why EEG oscillations and ERPs are related.

6.3.4   Filtered ERPs

Consequently some ERPs for the (above) described data will be shown. These grand-average ERP figures have a descriptive character and were computed for different conditions (encoding and retrieval) and different sub-samples (as described earlier) divided by IAF-peak and recognition performance. All the subsequent graphs show group-averages of the broad-band ERP (0.5 to 30 Hz) and the respective (individually adjusted and averaged) "Alpha"-ERP ((IAF - 4 Hz) to (IAF + 2 Hz)). An averaged standard and alpha ERP was computed separately for each subject (and each condition) which subsequently were combined to group averages. Enlarged versions of these graphs (with exact power and latency data) are attached in the Appendix (fig. A2-A5).
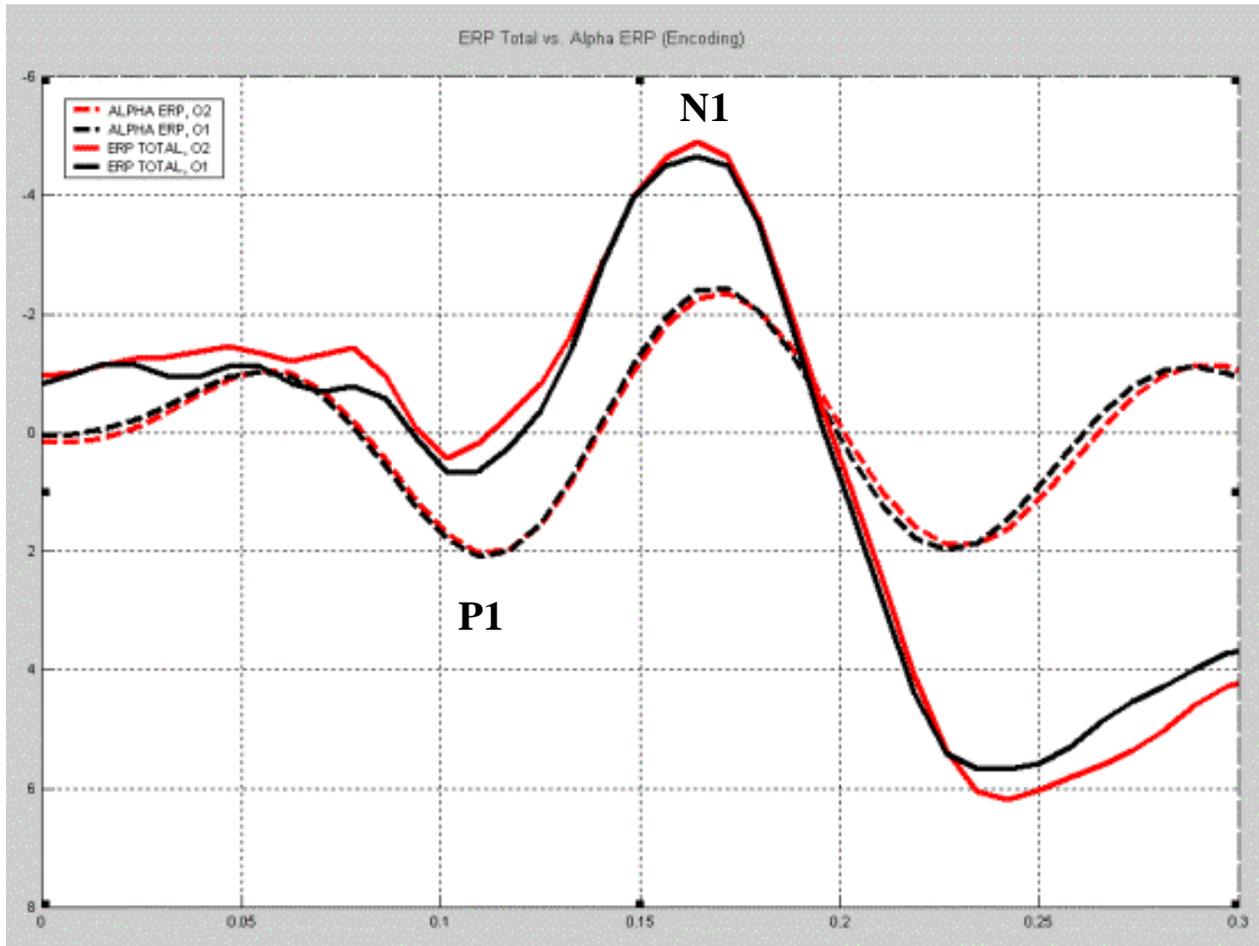
Figure 19. ERP Total vs. Alpha ERP during encoding (full sample)

The ERPs show two early components a positive peak at about 110 ms (termed P1) and a negative peak at about 160 ms (termed N1) which are strongly influenced by evoked alpha activity as can easily be seen by comparing the respective peaks of the ERP (Total) and alpha ERP.
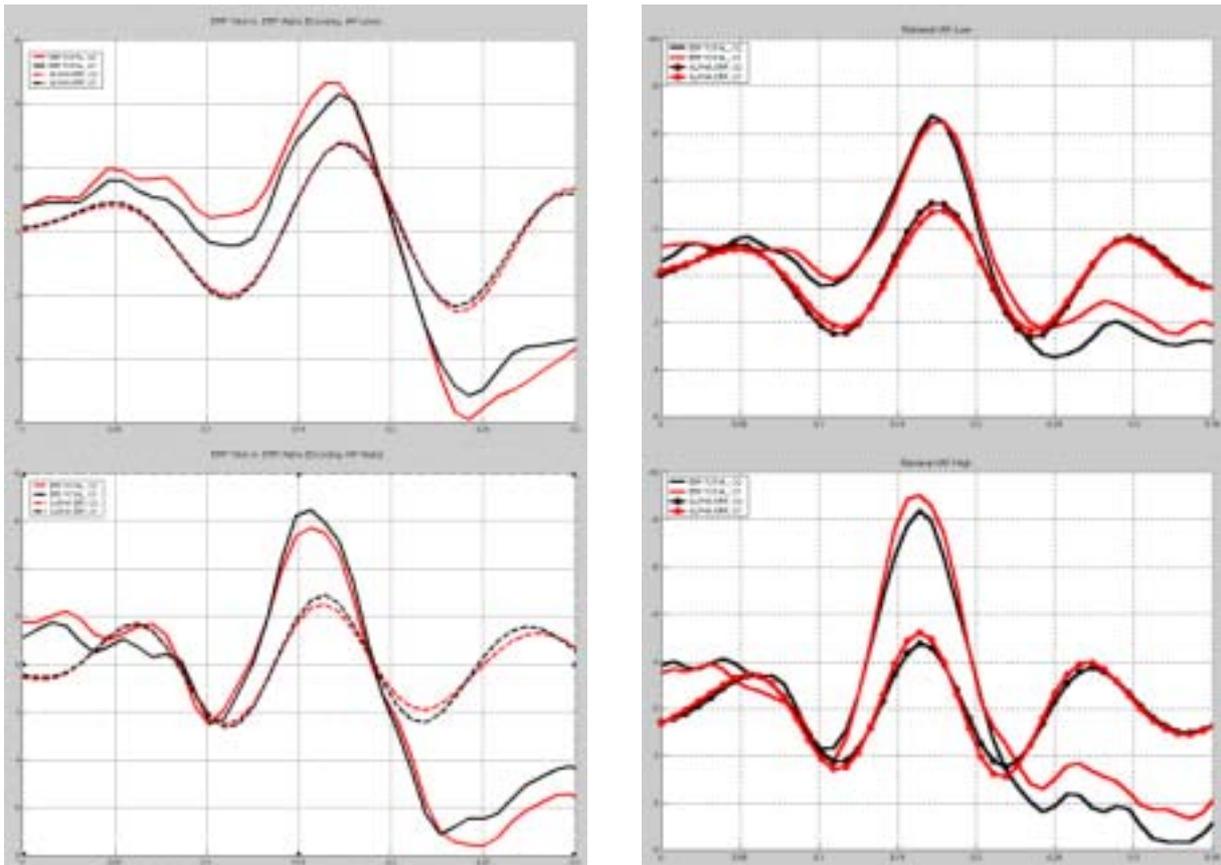
Figure 20 and Figure 21. ERP Total vs. Alpha ERP during encoding (left) and retrieval (right)

The upper graph shows IAF-Lows, whereas the lower one shows IAF-Highs. Each vertical stripline corresponds to steps of 50 ms. Note the earlier and enhanced P1-components for Ss with high individual alpha frequency (IAF).

Peaks with alternating polarity can be found even beyond the P1-N1 complex, far after 300ms, for an example see figure 22.
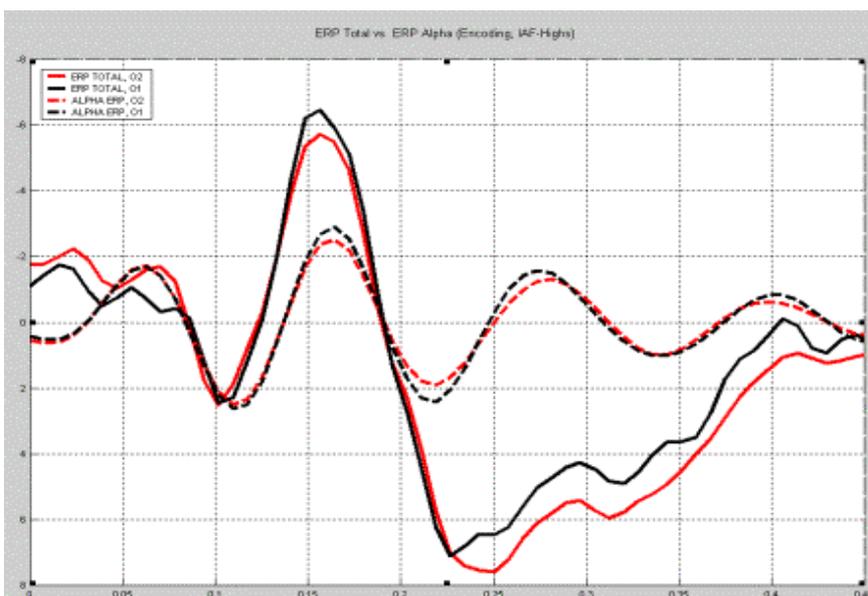
Figure 22. Peaks with alternating polarity

Shown is a standard-ERP and an alpha-ERP (during encoding for IAF-Highs). Note the correspondence of evoked alpha activity and the broad-band ERP even at 400 ms post-stimulus.

Figure 23 shows an averaged standard ERP (red line) and the individually adjusted subbands for a single subject (fore the encoding condition). The N1-component is highlighted, dotted lines extend the respective "subband-peaks".
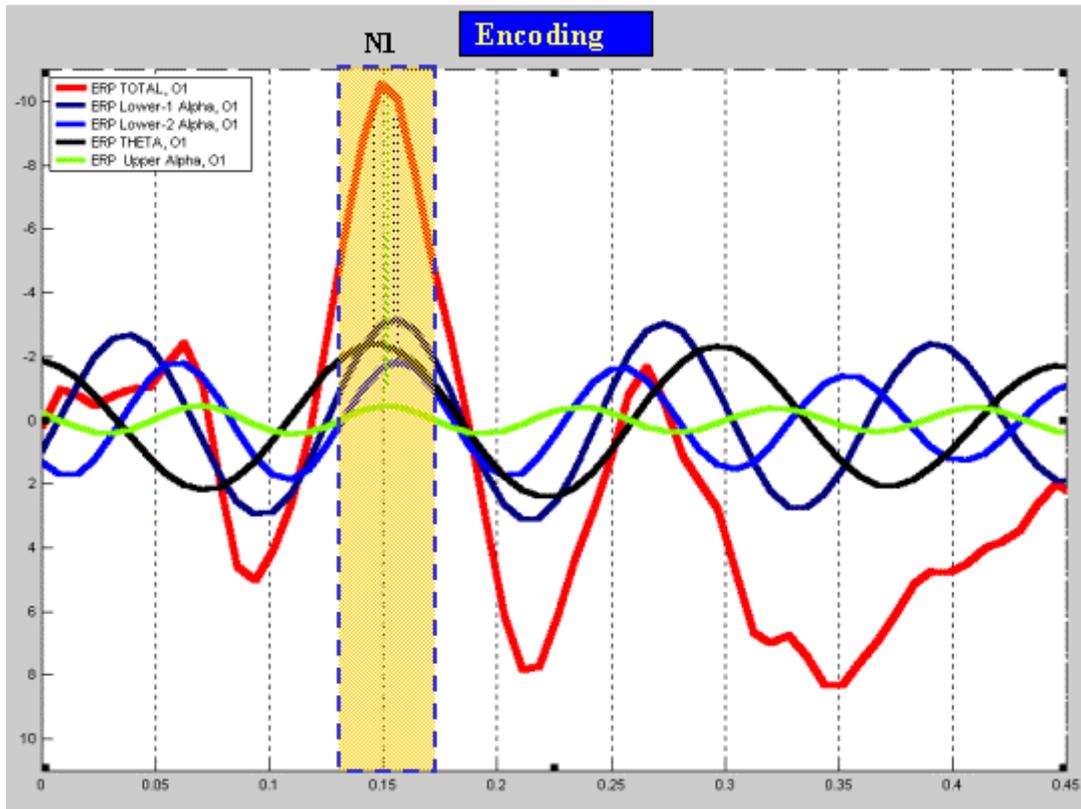
Figure 23. Transient phase-realignment during encoding (averaged ERP of a single subject)

The standard ERP (red line), as well as lower-1 alpha (dark blue), lower-2 alpha (blue), theta (black) and upper-alpha (green) –filtered ERPs at electrode site O1 are shown.

6.4   <u>Discussion</u>

The leitmotif of the present work is to demonstrate that event-related potentials (ERPs) might possibly be nothing more than the superposition of several "evoked oscillations". The fact that the early ERP components (P1, N1, P2) are sharp waves with alternating polarities clearly demonstrate that neural synchrony occurs in narrow time windows probably alternating between inhibitory and excitatory processes. This however, is exactly the way an oscillatory process is operating. Sometimes even cases with peak trains of alternating polarity far beyond the P1-N1 complex (as indicated by fig. 22) can be found.

Numerous studies indicate that the P1-N1 complex reflects sensory and early attentional processes. A very similar interpretation holds true for the (lower) alpha rhythm. Considering the data presented throughout this paper, the evidence for a link between early ERP

components and oscillatory processes seems to be intriguing, which should not only have become evident with the help of descriptive and correlational data but which also is remarkably reflected within the figures presented. Finally, I will try to recapitulate and discuss the results presented (above).

6.4.1 Evoked potentials, simply the superposition of "evoked rhythms"?

It was postulated earlier that ERPs might result from oscillatory brain activity reorienting and becoming phase-locked in response to a stimulus and furthermore, that every evoked potential may contain oscillatory responses in various frequency ranges depending on cognitive demands. Note the intriguing correspondence of alpha-ERPs and standard-ERPs. The evoked alpha-activity almost completely accounts for the P1-component for high IAFs (cf., fig. 19-22 lower graphs). Figure 23 on the other hand shows the strong phase realignment of all the subbands (lower-1 alpha, lower-2 alpha, theta and upper-alpha; individually adjusted by using IAF (cf. fig. 12B)) contributing globally to the N1-amplitude. But also note the reorganization of the two lower alpha bands (dark blue and blue line) with respect to the P1 and N2. The strong global reorganization and the transient phase-locking of these oscillations coincide exactly with the appearance of the N1-component, which fits nicely considering the postulated moment for encoding where theta appears to "lock in". Or in other words, it almost seems as if attention (lower-alpha acting as "agent") leads working memory (neuronally represented as theta) up to this crucial moment in time, which happens to show up as N1.

6.4.2 The relationship between IAF, P1-components and recognition performance

Most importantly, it could be shown that the P1 component appears earlier in time as a function of IAF (at occipital sites) for both encoding and retrieval. This relationship could be demonstrated both with significant correlations as well as illustrated graphically in figure 18, 20 and 21. Enhanced P1-amplitudes for high IAF is interpreted in means of increased phase-locking, as suggest much earlier (refer to fig.6). This evidence strongly favors the idea that the P1-component indeed might be equivalent to phase-locked alpha activity.

Basar (1998) and Doppelmayr et al. (1998) relate high levels of prestimulus (reference) alpha band power to decreased ERP-amplitudes or in other words to a strong degree of alpha suppression, whereas others constantly reported enhancements of P300 Polich (1997) and N1-to-P2 interpeak amplitudes (Barry, 2000). This study focused on early ERP-components reflecting sensory and attentional processes and our results suggest that there is indeed a close link between alpha power and ERP-characteristics. The results obtained from our study

demonstrate an inverse relationship between IAF-power and P1 (and N1)-amplitudes, that is higher IAF-power and decreased P1 (N1)-amplitudes, which is in accord with the results of Basar et al. and Doppelmayr et al., though they referred to pre-stimulus alpha band power.

A possible interpretation for this effect might be a very early (stimulus triggered) broad alpha band power decrease, also event-related desynchronization usually is not expected to occur before 300 ms post-stimulus. This, however might reside in the fact that a simultaneous decrease of phase-locking - as was schematically depicted in fig. 6 – has to occur, so that ERD can readily be observed. P2-amplitudes (e.g., at lead O1), on the other hand, show a trend towards enhanced amplitudes with higher IAF-power. This might be a crucial point for understanding the contradictory results reported by Basar et al., Polich, Brandt and Barry. Barry et al. (2000) report that higher levels of pre-stimulus alpha activity (at Pz) result in larger ERP components at Cz and Pz (in an auditory oddball paradigm). Interestingly though, their figure depicting ERPs as a function of low vs. high pre-stimulus alpha levels (cf., fig. 4, p.45) clearly show – similar to our results – that N1-amplitude decreases and P2-amplitude increases as a function of higher alpha activity. Note that they referred to N1P2 and N2P3 peak-to-peak amplitudes only, which might have blurred the effects as N1 and P2 seem to behave in an inverse manner regarding pre-stimulus alpha activity. It is not unlikely that later ERP-components might have a quite less close relationship to alpha activity (as compared to early P1/N2-components) or are even modulated as a function of other frequencies (e.g., P300 and delta-activity). In the study of Barry et al., P1-to-N1 peak-to-peak latencies (at Cz and Pz) again are considerably shorter (being about 65ms apart or 7.7 Hz) as N1 to P2 with its 90 ms interpeak latency (i.e., 5.6 Hz). However, the question remains open how far pre-stimulus alpha activity – which Brandt, Basar, Barry, etc. referred to – is comparable to a reference using alpha-power during a relaxed state ("IAF-power" before or after the tasks), as we did.

Whatever the direction of this effect might be, probably the most important point to make is the fact that they all (Basar, Brandt, Barry, Doppelmayr, Polich, etc.) found an effect of prestimulus (alpha) activity in the first place. This might reflect fluctuations in cortical activation levels of individuals, which are still heavily neglected and overlooked when discussing ERP-variance.

In the next step consider the significant relationship between recognition and IAF, that is higher individual alpha frequency positively correlated with enhanced recognition performance. Similar to the relationship between IAF and component-latencies, high recognition correlates significantly with earlier P1-components at occipital sites. Here we are

already confronted with a very interesting constellation of "interlocked" phenomena. Note the complex relationship between individual alpha frequency, – which already has been associated with memory performance (e.g., Klimesch, 1996) - recognition performance and earlier ERP-components. Given that it is suggesting that the speeded responses usually given from good memory performers are made pssoible due to the earlier ERP-components. Demonstrating a direct relationship between the neurobiological basis and behavior would be amazing.

Taken this evidence together (refer to tab. 5) we are confronted with an astonishing interplay between individual alpha frequency, P1-amplitude, P1-latency, individual alpha power and even a behavioral correlate, which is recognition performance (depicted in fig. 25).

Encoding			
P1	IAFHz	Recog	IAFPow
Recog	.311		
L-O2	-.296	-.364	.305
A-O2	.306		-.332

Table 5. Correlation-matrix highlighting the most important relationships (for P1 during encoding)

Once again, lets recapitulate:

With regards to (high) IAF we have significant correlation with memory performance (higher recognition), earlier ERP-components (P1) (at occipital site O2) and higher ERP-amplitudes (P1) (O2 again). It has to be emphasized that this all is true during visual encoding, which is strongly expected to be located occipital (right).

Given only that, we do not know if the enhanced P1-amplitude is due to a broad band power-increase or due to enhanced phase-locking. But, there is another important mosaic left. Note the significant correlation indicated at the lower right corner of table 5. This correlation implies that with an increase in individual alpha power the amplitude of the P1-component at lead O2 decreases. If even though alpha power decreases (working against a P1-amplitude enhancement) the amplitude of the P1 increases, there seems to be only one interpretation left, which is P1-amplitude enhancement due to increased phase-locking.

For the retrieval condition a very similar interpretation seems to be true, the only difference being that there seems to be a trend towards a shift of phase-locking to more parietal sites (Pz, P4). It was shown that, irrespective of the type of recognition, initial recognition operations occur with the predominant participation of the right hemisphere.

6.4.3 Underlying oscillatory activities substantially modulate ERP-components

Evidence is presented that early evoked ERP components (generated by the P1-N1 complex), have a frequency characteristic that lies within the theta and/or alpha frequency ranges (see table 6).

By interpreting peak-to-peak latencies as frequencies we found that

    a) P1-to-N1 peak-to-peak latencies vary typically between 9 and 11 Hz (reflecting alpha)

    b) whereas the N1-to-P2 complex lies within a narrow frequency window around 7 to 8 Hz (reflecting theta)

P1 to N1	"Alpha"						
N1 to P2	"Theta"						
	Mean	**SD**	**N**		**Mean**	**SD**	**N**
ENCODING				**RETRIEVAL**			
P3 P1-N1	10,259	3,51	33	**P3 P1-N1**	**10,694**	6,12	32
P3 P1-P2	7,904	1,62	33	**P3 P1-P2**	7,883	2,31	32
P3 N1-P2	7,084	2,17	34	**P3 N1-P2**	7,375	2,72	32
PZ P1-N1	10,867	3,94	30	**PZ P1-N1**	**11,079**	6,03	31
PZ P1-P2	7,922	1,43	30	**PZ P1-P2**	8,416	3,22	31
PZ N1-P2	7,085	2,63	34	**PZ N1-P2**	7,881	3,41	33
O1 P1-N1	10,043	3,76	32	**O1 P1-N1**	10,053	4,02	31
O1 P1-P2	7,938	1,64	32	**O1 P1-P2**	8,196	1,94	31
O1 N1-P2	**6,905**	1,54	34	**O1 N1-P2**	7,912	2,32	33
O2 P1-N1	9,786	3,13	33	**O2 P1-N1**	8,751	2,87	33
O2 P1-P2	7,699	1,35	33	**O2 P1-P2**	7,394	1,54	33
O2 N1-P2	**6,804**	1,83	34	**O2 N1-P2**	7,063	2,17	33

Table 6. Peak-to-Peak latencies interpreted as alpha and theta activity

    It is interesting to note that during retrieval P1-to-N1 peaks are closer to each other at parietal sites (P3, Pz), whereas N1-to-P2 "frequencies" at occipital sites (O1, O2) are substantially slower during encoding as compared to the retrieval condition.

    If the observed **N1-P2 peak-to-peak latency** between 62 and 72 ms is interpreted as a half period of an oscillation, these peaks can be interpreted in terms of a fast theta or slow alpha wave with a period of 144 ms and a frequency of 6.9 Hz (or 124 ms and 8.1 Hz). Note that peak-to-peak latencies of the N1-P2 complex show faster frequencies for retrieval at all electrode sites. The assumption is that a theta-like system is needed for the encoding of information (as suggested by Klimesch, 1996) and that during retrieval the demand for this slower oscillatory activity already vanishes, therefore the N1-P2 peaks are not "moved apart" (by an underlying theta oscillation) with the same strength as compared to encoding. As suggested at occipital leads (O1, O2) where visual encoding is most strongly expected, the N1-P2 complex is slower during learning (6.9 Hz; 6.8 Hz) as compared to retrieval (7.9 Hz; 7.1 Hz).

Using the same logic for the **<u>P1-N1</u>** complex, a **<u>peak-to-peak latency</u>** of about 50 ms can be interpreted as alpha wave with a frequency of about 10 Hz. Peak-to-peak latencies of the P1-N1 complex show faster (upper-alpha) oscillatory activity for the retrieval condition at parietal sites (Pz, P3) where recognition is thought to take place (10.7 and 11.1 Hz). This result agree with the proposal first made by Klimesch (e.g., 1996), which states that during a retrieval task a neuronal shift to a state of "search and retrieval" reflected by an transient increase in upper-alpha activity can be observed .

For the <u>retrieval task</u> event-related alpha decrease (broad band alpha collapses) but increased phase-locking in response to a stimulus is expected. As search and retrieval processes are engaged upper-alpha activity is thought to increase. As lower alpha (attentional) and upper alpha for retrieval are thought to superimpose on each other increased **<u>P1-N1 peak-to-peak amplitudes</u>** are expected during retrieval. Indeed the results show increased P1-N1 peak-to-peak amplitudes (at all sites except Fz and Pz); refer to table 3 and figure 24. Contrary to our expectations however, phase-locking increases not only in task-relevant cortical regions (e.g., parietal for retrieval), but undifferentiated for (almost) all leads.

Table 2 and 3 indicate the slowed oscillations during <u>encoding</u> (N1-P2 peak-to-peak latency enhanced as compared to retrieval) and the increase in **<u>N1-P2 peak-to-peak amplitudes</u>**, which is interpreted as event-related theta synchronization for the "encoding of new information" (i.e., enhanced phase-locking within the theta range). Figure 24 shows schematically the enhanced N1-to-P2 interpeak amplitudes, which can be observed during encoding at all electrode sites except Fz (for complete data see table A9).

Encoding:
(Recognition „Highs")

N1-to-P2 peak-to-peak power Theta increases
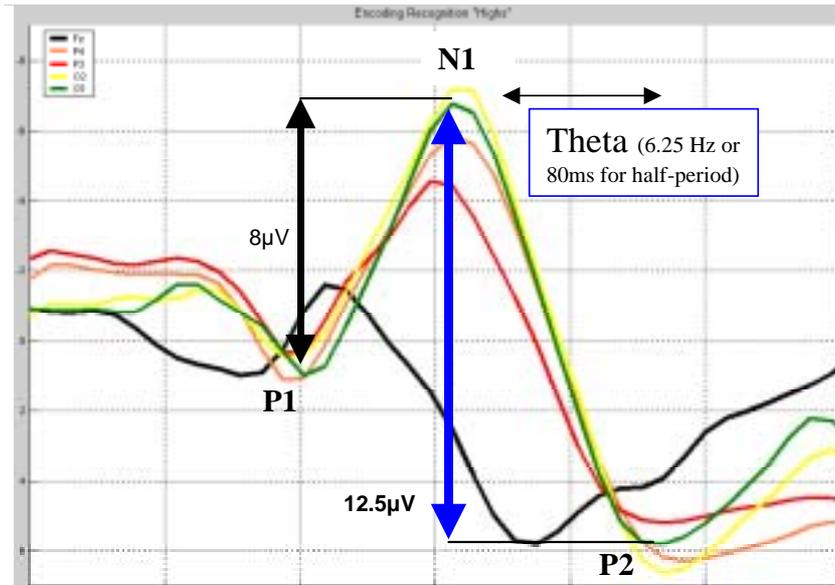
Retrieval:
(Recognition „Highs")

P1-to-N1 peak-to-peak power Alpha increases
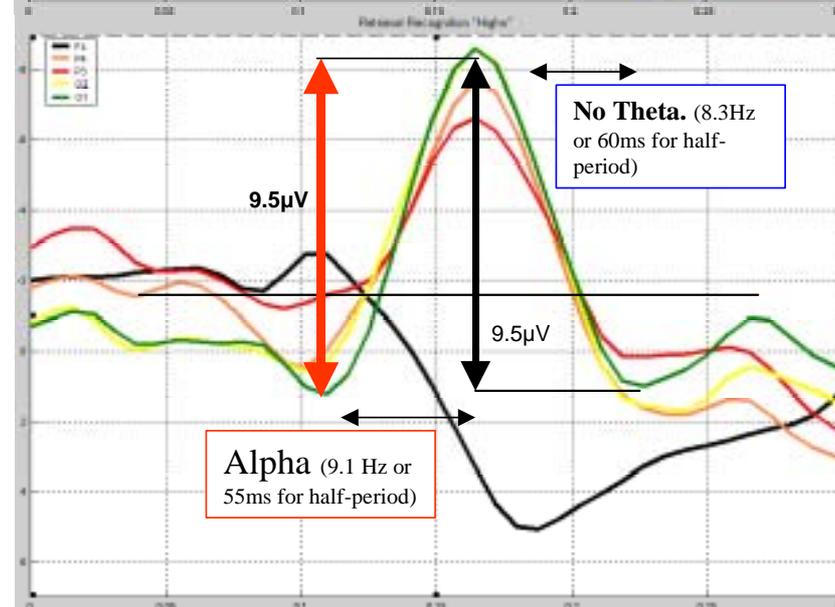
Figure 24. Task specific modulation of brain oscillations and ERPs during encoding and retrieval

Note that during retrieval N1-P2 corresponds to a theta oscillation, and respective peak-to-peak amplitudes are enhanced. However, in the retrieval condition P1-N1 peak-to-peak amplitude increases. Note also the countercourse of the frontal lead (Fz, black line).

Furthermore, it could be shown that there is a significant relationship between **recognition and N1-P2 peak-to-peak latencies**. This effect happened to be in the expected direction, with better performers showing slower N1-P2 frequencies, interpreted as an increase in underlying theta oscillators (schematically depicted in fig. 25). These correlations were significant at parietal (Pz, P3, P4) and parietooccipital sites (PO3) (cf., table A7-A8).
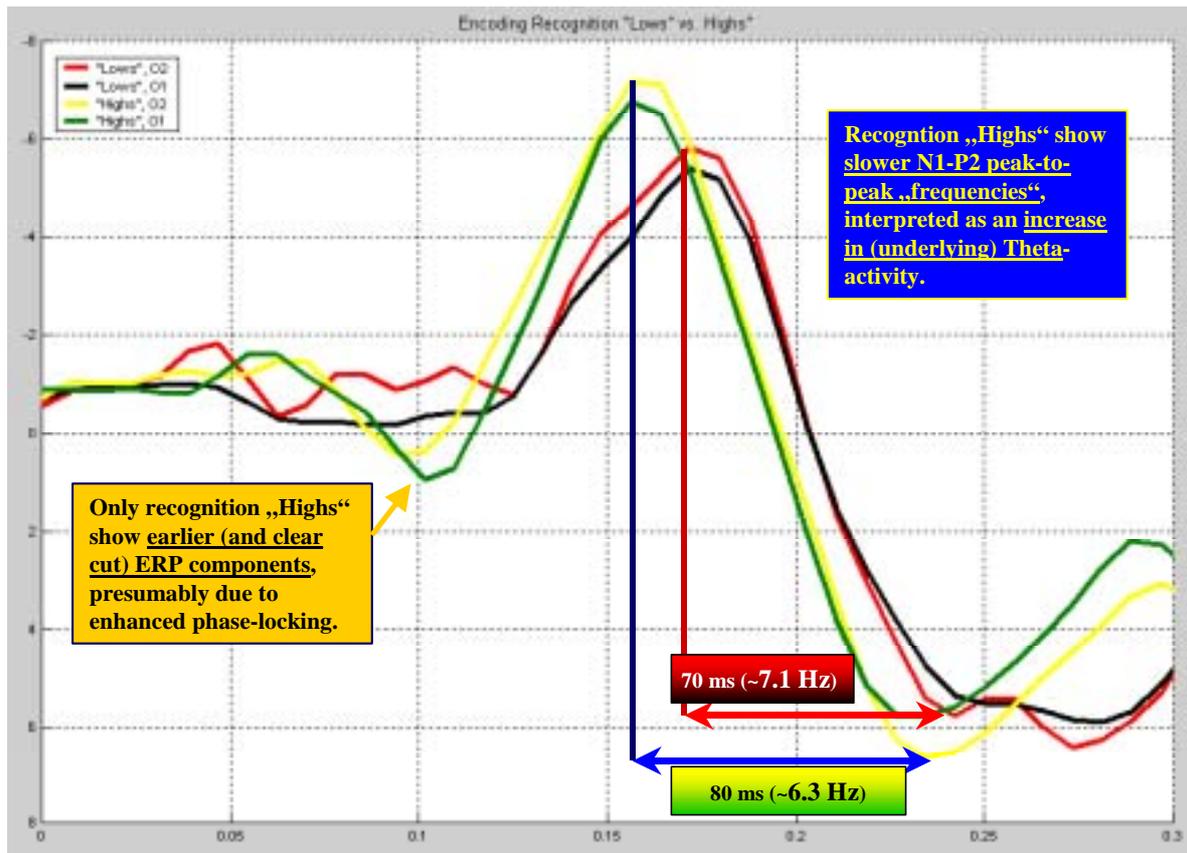
Figure 25. Graph showing schematically the results for recognition low vs. high

Note the earlier (and clear cut) P1-peaks for "Highs", as well as the increased N1-to-P2 interpeak latency.

It is important to note that the figures presented in the discussion (and result) sections - in the first place – are thought as a tool for schematically emphasizing the results discussed. Although the graphical means are computed with subsamples of the actual data, they may show quite deluded results, as subjects with high power might considerably blur graphs (though it was attempted to control for these effects as far as possible).

Given the data (see fig. 15-17 and Appendix table A5 for complete listing) it looks like brain oscillations "swash" from anterior to posterior regions, starting with high frequencies – e.g., the C1-component seems to be a "gamma-component" - on which slower ones like alpha and then theta superimpose or "join in".

Not mentioned so far is a somewhat surprising relationship, which might suggest a neuronal dissociation between frontal cortical regions (electrode site FZ) and more posterior ones. While local IAF-Power correlates negatively with P1, N1 and P2 amplitudes at posterior sites, the opposite holds true for electrode site Fz (tab. A1-A3). Taking a look at figure 24 the frontal site (black line) is progressing in time with almost a counter course to parietal and occipital leads. A figure 8-shaped polarity-reversal might favore the same neuronal source at

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different depths, but the additional shift in phase between those sites rather suggests different neuronal generators.

In particular data from Knight et al. (in press, as cited in Handy et al., 2001) suggest that prefrontal cortex (Brodmann's areas 9 and 46) modulates processing in posterior cortical areas via parallel excitatory and inhibitory reafferent projections. Top-down inputs from prefrontal cortex are intimately involved in mediating sensory processing in extrastriate cortex, in a sense it can be understood as an "attentional controller" allocating the "benefits of attention", although it remains resolved how these effects are implemented. "One possibility is that these top-down effects on early visual processing are subserved by a corticothalamic network involving the pulvinar nucleus, which may act to provide an amplification signal to those posterior visuocortical areas which are processing inputs from attended spatial locations" (LaBerge, 1995). The enhancement of ERP-components via the pulvinar nucleus – very early in time- call attention to the fact that nuclei in the thalamus already conduct basic selection or filtering processes, long before one can be conscious aware of those sensory stimuli.

Accounting for the objection that the positive correlation between individual alpha frequency and the behavioral data of correctly recognized items might be come about due to participants' tiredness or fatigue alpha peaks were calculated throughout the whole experiment. Comparing power spectrums with eyes-closed at rest before the tasks, spectrums from reference intervals during the task, and eyes-closed resting after the tasks revealed no significant changes. Particularly, the transition to slower frequencies for participants denoted "bad memory performers" or "lows" was checked, as that would have meant worse performance due to fatigue and not as function of IAF, per se.

And finally, could it possibly be that phase angle and not alpha frequency per se accounts for the variations in ERP latency and amplitude? The substantial influence of pre-stimulus alpha phase angle on ERP components has already been demonstrated e.g., for the N1 by Brandt (1997). Commonly ERP-components are considered time-locked but not phase-locked (!) to a stimulus, or in other words it is assumed that there are no systematic (and substantial) prestimulus changes in spontaneous EEG which would have to be considered. If brain oscillations are assumed to be in rather random order preceding a stimulus, equally often a more advantageous as disadvantageous phase angle should result for a high alpha frequency (IAF) as compared to a lower one. Actually, only if there is already some kind of phase alignment preceding the stimulus variations in IAF would systematically covary with phase

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angle. That on the other hand would not really make a difference for the proposed alternative ERP-generation model (cf. fig. 6), which postulates the reorganization of ongoing EEG activity as the "true source" for ERPs.

7   Evidence from classical P1-N1 literature (descriptive)

7.1   Introduction

Visual attention tasks were reviewed, because an overwhelming number of these studies focused on the early P1/N1 ERP components. As the selected studies experimentally manipulate attention differences in attention should also become evident in terms of brain oscillations (or the "alpha system"). Stimuli at attended locations are expected to "recruit" more rigidly the "attentional spotlight" and thus consequently enhanced alpha activity and phase-locking should be observable. That again, should be accomplished by measuring peak-to-peak amplitudes (P1-to-N1) for attended vs. unattended stimuli/locations. Furthermore, it was of interest if the same relationship as reported for the experimental work presented earlier could be found; that is an alpha-like rhythm for the P1-to-N1 latencies and a theta-like rhythm for N1-to-P2 peak-to-peak latencies. Given the evidence already presented it was tempting to assume a pronounced alpha oscillation (visible in the averaged ERP) from the P1 to N1 peak, especially over occipital sites (O1, O2), which possibly even would stay over longer periods in time. This is because visual attention is known to be most prominent around the striate and extrastriate areas of the occipital lobe and, thus the (proposed) closely linked attentional alpha system should show up with most pronounced activity there.
We assumed that even if higher cognitive processes would superimpose on the ERP waveform the early P1/N1 complex would be rather unaffected. Further, dependent upon task or cognitive demands different brain oscillations were assumed to "come in" at different stages in time (e.g., Theta at the N1).

7.2   Method

At first the literature was reviewed for ERPs, P1-/N1-components and visual attention. Tasks and paradigms considered suited for an analysis were for example spatial selective attention, signal detection or visual search paradigms, as they all seem to share common attentional mechanisms. Of course it was tendering to use studies from people being busy in ERP attention research for years and years like Clark, Hillyard, Luck or Mangun to just mention some of them. The reason we decided to choose the visual domain for this review was rather arbitrarily, though admittedly we supposed similar and comparable results (with respect to the obtained data from the visual recognition task) at least for the early P1-/N1-complex. Therefore, primarily posterior (occipital, parietal) sites were analyzed for the selected literature.

However, it is assumed that the experimental outcome doesn't really rely on the studies (or the domain) actually used and should be quite similar (regarding the P1-/N1-complex) for other ERP-studies studying attention. Although simple structured, well controlled and/or good studied tasks should be favorable, cause there attention can show up straight without being overlapped by higher-order cognitive processes.

Then the selected studies were screened for practical and appropriate figures. Studies with figures of ERPs being too small to be measured confidently on a scale of at least 5-10 ms (for judging ERP-peaks) were excluded (see fig.26 for an excluded figure). Suited figures were scanned and measured using self-made scaling-templates (for an example see fig. A6) or simply manually measured with a ruler. For examples of suitable and actually used ERPs refer to figure 3-5.
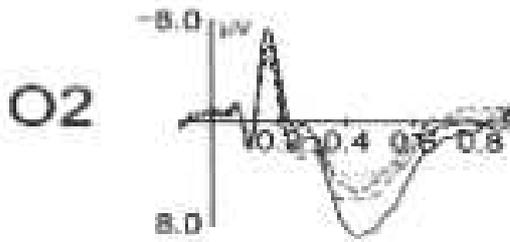
Figure 26. Example of an unusable ERP figure
(from: Böttger & Herrmann, 2001)

Table 7 depicts the respective results including a number of informations (from left to right): study name, task (short description), number of subjects in study (N), age (mean or range), stimulus probability, inter-stimulus interval (ISI), P1-, N1- and P2- latency and power, the computed P1-to-N1 and N1-to-P2 peak-to-peak latency (in Hz) and power, and finally the electrode sites reported (PL for parietal left, PR parietal right, OL occipital left, OR occipital right).

7.3   Results

7.3.1   Frequency characteristics of the waveform: Peak to peak latencies

If the P1- N1 peak to peak latency of about 50 ms is interpreted as a half period of an oscillation, these peaks can be interpreted in terms of an alpha wave with a period of 100 ms and a frequency of 10 Hz. The results show a mean of 10 Hz ($\underline{SD}$ = 2.9) for the P1-to-N1 peak-to-peak amplitude and 7.5 Hz ($\underline{SD}$ = 2.2) for the N1-to-P2 interpeak latency.

It is conspicuous that the composition of "unattended" stimuli is considerably slower for the N1-to-P2 interpeak latency, $\underline{M}$ = 7.0 Hz ($\underline{SD}$ = 2.5), as compared to "attended" stimuli $\underline{M}$ = 8.2 Hz ($\underline{SD}$ = 1.7).

7.3.2   Frequency characteristics of the waveform: Peak to peak amplitude

Overall the mean interpeak amplitude for P1-to-N1 is 3.7µV ($\underline{SD}$ = 3.1), and 5.2µV ($\underline{SD}$ = 3.1) for N1-to-P2. Comparing the composite of "attended" vs. "unattended" it is interesting to note that attended show a P1-to-N1 amplitude of 4.3µV ($\underline{SD}$ = 3.1), whereas unattended show 3.4µV ($\underline{SD}$ = 3.3). N1-to-P2 amplitude is roughly the same for both attended ($\underline{M}$ = 5.4, $\underline{SD}$ = 2.8) and unattended ($\underline{M}$ = 5.2, $\underline{SD}$ = 3.6).

ERPs obtained under short interstimulus intervals (ISIs) show a mean P1-N1 peak-to-peak amplitude of 1.8µV ($\underline{SD}$ = 0.8), and 3.2µV ($\underline{SD}$ = 2.3) for N1-to-P2. ERPs for long ISIs have a mean P1-N1interpeak amplitude of 4.8µV ($\underline{SD}$ = 3.1), and 6.1µV ($\underline{SD}$ = 2.7) for N1-to-P2.

7.3.3   "A glimpse into the auditory domain"

In a classical dichotic listening experiment by Hillyard et al. (1995) stimuli were presented in a rapidly sequential order to either the left or right ear. Participants had to respond to slightly differing acoustic stimuli by pressing a button. The (P1-N1) interpeak-latency was about 66 ms (for both ears), corresponding to a full period of 132 ms or 7.7Hz. The same was true for P1-to-N2, being somewhat faster for the left ear (60 ms corresponding 8.3 Hz). The difference for the two attention conditions, as expected, became obvious looking at peak-to-peak amplitudes. For the left ear, P1-N1 interpeak-amplitude was about 1.63 µV (attended) vs. 0.88 µV for the unattended, and for the right ear 1.5 µV vs. 0.8 µV, respectively.

Table 7. Publication Table of P1/N1 studies in the visual domain

7.4   Discussion

It was not aim of this review to be particularly comprehensive and complete, rather this work should be regarded as a pilot study checking for the feasibility and usefulness of a much broader literature review.

As each stimulus automatically triggers some kind of attentional response the question arose in which means "unattended" locations or stimuli should be different from attended ones. The most plausible explanations seems to be that, less attentional involvement should result in less regular or less phase-locked alpha activity and this should become evident in diminished peak-to-peak amplitudes. And indeed enhanced P1-N1 peak-to-peak amplitudes were found for attended (vs. unattended) in this brief literature review.

Besides simply looking at the difference between attended and unattended "standard" stimuli, we also hoped that attention – as observable in peak-to-peak amplitudes - would vary as a function of interstimulus interval (ISI) and stimulus probability (p_s). A difficulty arose, because most of the studies only include figures of their standard stimuli, thus the (assumed) enhanced attentional involvement to target stimuli (low p_s) could not be measured. Furthermore, it was assumed that short ISIs attenuate component amplitudes, because (broad) alpha activity desynchronizes in response to each stimulus. This however could be examined, and is indicated by the greatly enhanced P1-N1 and N1-P2 peak-to-peak amplitudes for long (>800 ms) ISIs.

The fact that the P1 shows an occipital maximum (even in this brief review), supports the notion of its generator in the visual cortex. But as the P1 does not invert polarity (like the C1), it is assumed to arise from extrastriate areas. Thus it seems that the ventro-lateral extrastriate cortex is the location where visual-spatial attention affects stimulus processing in the first place (Rugg, 1995, p. 54). Rugg (1995, p. 55) notes that „Presumably the visual N1 reflects activity of several underlying brain processes whose electrical signals overlap temporally and spatially on the scalp. " Thus, as one proceeds from anterior to posterior scalp regions peaks of the N1 component(s) have longer latencies (cf., fig. 16). Although the P1 attention effect almost certainly represents a modulation of perceptual processing, it is not clear exactly which specific areas of visual cortex are subject to attentional control. Studies which attempted to account for the neuroanatomical sources of the ERP attention effects, usually proposed neural generators for P1 and N1 somewhere in extrastriate areas. Mangun and Hillyard (1990a), Mangun et al. (1993) or Clark and Hillyard (1996) suggest ventrolateral extrastriate cortex (and parietal sites, respectively) as the sources for the attention sensitive P1 and N1 effects. Heinze and colleagues (1994, in Gazzaniga, 2000) performed a combined ERP/PET session

for a typical ERP attention experiment. They found that the P1 attention effect was associated with both an increase in blood flow in the ventral occipital lobe in the posterior fusiform gyrus and a consistent P1 generator source in this region by dipole modeling. A second area was suggested in dorsal occipital areas by Woldorff et al. (1997, in Luck et al., 2000). Although the specific areas affected by attention varies among the experiments, the combined ERP and PET data strongly indicate that early perceptual attention effects take place in (lateral) extrastriate visual cortex. The results presented as well suggest P1 and N1 sources somewhere between parietooccipital and occipital sites (see brainmap figures 15-17), though the task was also a visual attention task, it differed with respect that it was not a visual selective or spatial attention but a visual recognition task. The question thus remains how closely the two generators for the P1 visual attention effects comply with each other.

Although it is long known that spatial attention can selectively modulate processing in extrastriate cortex, recent ERP research has revealed another interesting effect. In particular, Handy and Mangun (2000) found that these classical effects of attention depend directly on the perceptual load of a given task. In an spatial cuing paradigm the magnitude of attentional modulation in the P1 and N1 components increased positively with the perceptual load of target items. The results suggest that these effects of attention within extrastriate cortex can be ascribed to resource allocation, where a greater proportion of limited-capacity attentional resources are allocated to the cued location under high vs. low perceptual load. It seems that within the low load condition enough resources are available for also processing stimuli at unattended locations (N1 difference is minimal), whereas in the high load condition the benefit of being within the "spotlight" of attention is crucial for a stimulus to be processed at all (N1 difference, reflecting "attentional benefit" is high). Handy et al. (2001) emphasize the importance of this direct and positive relationship between neuronal response and attentional resource allocation for understanding selective attention.

Regarding the alternative (ERP) model suggested throughout this paper, the high load condition exerts higher attentional demands on the neuronal system which shows up as increased phase-locking of (lower) alpha activity, and thereby causes higher ERP (P1, N1) amplitudes.

Although it is true that the evidence from visual (spatial) attention studies discussed here is quite different from the visual recognition task presented earlier on, one has to keep in mind the common ground of those two. Both are thought to be heavily dependent on visual attention and to have corresponding sites of attention (i.e., occipital).

Taking a glimpse at the auditory domain similar main-effects as in the visual seem to hold true. The only real exception are the earlier ERP-components, being already different for the attended condition even before 50ms. The results from Hillyard et al. (1995) in there dichotic listening experiment again could be interpreted in means of increased phase-locking of (lower) alpha activity for conditions with enhanced attention engaged.

As it is well known that young children and people with neurological disorders have lowered alpha activity it would be interesting to also review studies examining these groups and look for diminished P1/N1 peak-to-peak amplitudes.

8   General discussion and follow-up proposal

Evidence was presented that early evoked ERP components (i.e., P1-N1, N1-P2 complex) share a remarkable amount of characteristics with evoked brain oscillations, especially in the alpha band. Just recall the fact that early components are sharp waves with alternating polarities, which probably demonstrates that neural synchrony alternates between inhibitory and excitatory processes and which remarkably is exactly the way an oscillatory process is operating. Or think back that the P1-N1 complex reflects sensory and early attentional processes, just as suggested for the alpha rhythms.

Because it could be demonstrated that the "P1-N1-P2" complex is indeed the manifestation of an oscillatory process in the alpha (and theta) frequency range these early evoked EEG components must be considered not only time locked but also phase locked with respect to a stimulus.

I hope that this work was able to transport the main idea, though I am completely aware of the fact that the suggested "alternative model" for ERP-generation (with all its assumptions and interpretations) might not be shared by the whole field and might even be looked at somewhat distrustful.

After having demonstrated the significant relationship between ERPs and brain oscillations in a descriptive and correlational sense the next step to make would be a causal one. If it could be shown that there is a causal relationship between alpha activity, ERPs and possibly even (recognition) performance, this would literally boost the acceptance for the postulated "oscillatory model".

Thereby, a phenomenon commonly known as "photic driving" could be potentially useful. When the brain is exposed to the stimulation of a certain wave, it tends to adopt to this wave's predominant pattern, as long as the stimulation lasts. This well known physiologic response to intermittent photic stimulation is called photic driving. Although the posterior (occipital) EEG is usually "driven" by photic stimulation in normal people, people with occipital damage either have no photic driving, or when it happens, asymmetric photic driving; but still not even all "normal" people are susceptible to photic driving.

For example, it would be very interesting if flickering light (between 8 and 12 Hz) would be able to directly modulate alpha activity and that consequently should modulate the appearance of early evoked ERP components. Most compelling, however would be to demonstrate further the causal influence of alpha activity (high vs. low) on behavioral measures such as recognition performance. Presumably, even the study presented in the

experimental chapter could be replicated by simultaneous (rhythmic) photic stimulation, though being methodical difficult.

Given photic driving and the resonance phenomena described e.g., by Herrmann (2001) it seems quite important to bring to mind a simple but perhaps nontrivial qualm. The commonly used device for presenting visual stimuli in EEG-research are computer monitors. Note that monitor resolutions commonly vary between 80 and about 120 Hz, thus having their harmonics between 8 and 12 Hz. This however, could be potentially confounding with alpha activity, which traditionally varies in the frequency range of about 7.5-12.5 Hz (e.g., Klimesch, 1999). Therefore it seems important to experimentally control for possible effects or at least to be aware of possible influences.

So perhaps EEG-studies are already commonly pairing their tasks with "photic stimulation" without recognizing…

9   Appendix

Electrode sites
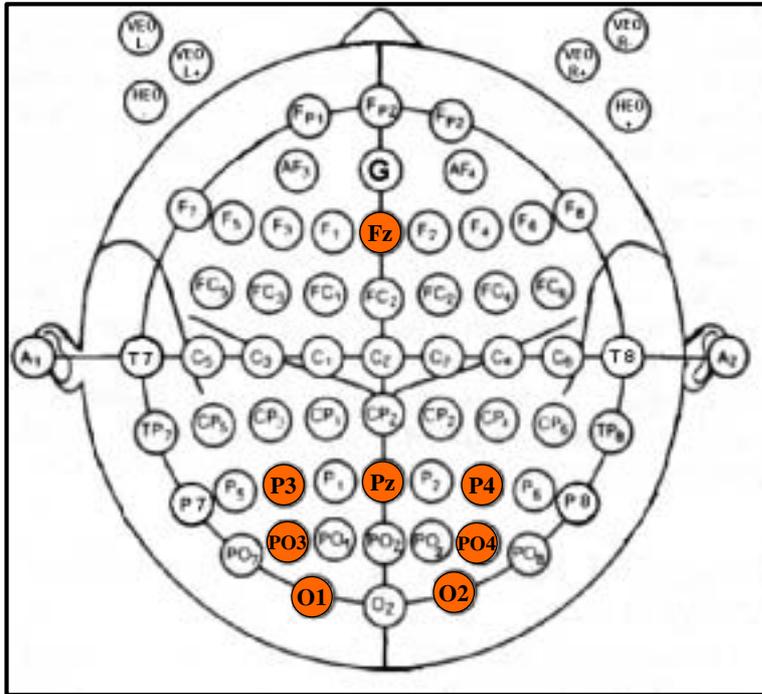
Figure A 1. Schematic representation of analyzed electrode sites

Encoding										
P1	IAFHz	Recog	Age	IAF-Power	IAF-Fz	IAF-Pz	IAF-P3	IAF-O1	IAF-O2	L-Pz
IAFHz										
Recog	.311									
Age										
IAF-PO4			-.374							
L-PO4	(-.294)	-.327		.495*						
L-O2	-.296	-.364		.305						
A-Fz			(-.294)		.356					
A-Pz		-.415								.399
A-P3				-.299		-.315				
A-PO3	.295									
A-O1	.351							-.304		
A-O2	.306			-.332					(-.285)	

Retrieval										
P1	IAFHz	Recog	Age	IAF-Power	IAF-Pz	IAF-P3	IAF-PO3	IAF-PO4	IAF-O1	L-Pz
L-Pz	-.352	-.296								
L-P4		-.325								
L-PO3				.313			.306			
L-PO4	-.326	-.404*		.412*				.375		
L-O1	-.311								.300	
L-O2	-.371	-.420								
A-Fz		-.409	-.292							
A-Pz				-.375	-.352					.300
A-P3				-.380		-.480				
A-PO3	.327									
A-O1	.331			-.335					-.303	
A-O2	(.274)			-.293						

Table A 1. P1 intercorrelation-matrix

Encoding						
N1	Recog	IAF-Power	IAF-Pz	IAF-P4	IAF-PO3	L-Pz
L-P4	-.316			.331		
L-PO4		.416*				
L-O2		.346				
A-Pz			-.317			.301
A-PO3		(-.263)			-.335	
Retrieval						
N1	Recog	IAF-Power	IAF-Pz	IAF-P4	IAF-PO3	IAF-O2
L-P4	-.301			.302		
L-O2						.348
A-Pz			(-.284)			
A-PO3					-.304	

Table A 2. N1 intercorrelation matrix

								Encoding						
P2	IAFHz	Recog	Age	IAFPow	IAF-Fz	IAF-P4	AF-PO4	IAF-O2	L-Pz	L-P3	L-P4	L-PO3	L-PO4	L-O1
L-Pz		.300	.383											
L-P3			.312											
L-P4						.318								
A-Fz					.309									
A-P3										.411*				
A-P4											(.284)			
A-PO3		.295											.314	
A-PO4	.332													
A-O1		(.269)												
A-O2								.400						
								Retrieval						
P2	IAFHz	Recog	Age	IAFPow	IAF-Fz	IAF-O1	AF-PO4	IAF-O2	L-Pz	L-P3	L-P4	L-PO3	L-PO4	L-O1
L-Fz				(-.270)	(-.258)									
L-PO4							-.395							
A-Pz									.444*					
A-P3										.517*				
A-P4											.423*			
A-PO3												.502*		
A-PO4	(.288)												.318	
A-O1				(.282)		.363								.471*
A-O2								.374						

Correlation is significant at the 0.05 level (1-tailed)
*. Correlation is significant at the 0.01 level (1-tailed)
( ) Nearly significant (.050-.065)

Table A 3. P2 intercorrelation-matrix

	Mean	SD	N
IAFPOWER	11,31	12,31	34
IAFFZ	4,39	5,70	34
IAFP3	10,97	10,45	34
IAFPZ	13,60	15,11	34
IAFP4	13,68	15,25	34
IAFPO3	12,06	15,08	34
IAFPO4	11,22	15,06	33
IAFO1	9,60	11,58	34
IAFO2	11,23	12,56	34

Table A 4. Local IAF-Power

P1 (Encoding)	Mean	SD	N	P1 (Retrieval)	Mean	SD	N
LFZ	88,90	14,97	29	LFZ	91,52	18,52	35
LP3	105,59	18,13	33	LP3	102,90	22,30	35
LPZ	102,86	20,93	30	LPZ	97,30	20,12	33
LP4	104,74	16,47	32	LP4	101,56	19,14	34
LPO3	106,77	18,18	33	LPO3	108,48	20,56	35
LPO4	109,90	15,88	30	LPO4	113,74	19,35	34
LO1	103,51	21,11	32	LO1	108,66	21,78	33
LO2	108,43	17,33	33	LO2	107,59	22,10	35
AFZ	1,26	2,10	29	AFZ	0,23	2,79	35
AP3	2,06	3,21	33	AP3	0,28	3,72	35
APZ	0,66	3,13	30	APZ	-1,57	3,13	33
AP4	2,47	3,06	32	AP4	1,27	3,57	34
APO3	2,97	3,24	33	APO3	2,13	3,48	35
APO4	3,10	3,31	30	APO4	3,28	3,93	34
AO1	2,48	3,45	32	AO1	2,69	3,64	33
AO2	2,34	2,90	33	AO2	2,73	3,01	35
N1 (Encoding)	Mean	SD	N	N1 (Retrieval)	Mean	SD	N
LFZ	134,28	23,93	32	LFZ	130,80	23,54	35
LP3	159,70	18,47	34	LP3	161,31	21,83	34
LPZ	152,57	26,80	34	LPZ	150,67	27,69	35
LP4	163,37	17,46	34	LP4	166,13	17,45	34
LPO3	163,14	15,48	34	LPO3	170,09	13,93	35
LPO4	169,51	18,27	33	LPO4	174,86	13,33	34
LO1	160,16	15,65	34	LO1	166,74	16,51	35
LO2	163,83	19,18	34	LO2	170,31	12,54	35
AFZ	-2,46	2,69	32	AFZ	-3,49	3,12	35
AP3	-5,74	4,46	34	AP3	-8,00	4,45	34
APZ	-5,07	4,64	34	APZ	-6,67	3,99	35
AP4	-6,29	4,34	34	AP4	-8,13	4,35	34
APO3	-6,25	4,01	34	APO3	-8,57	4,62	35
APO4	-6,09	4,33	33	APO4	-7,41	4,51	34
AO1	-6,00	3,93	34	AO1	-7,79	4,39	35
AO2	-6,21	3,80	34	AO2	-7,49	4,07	35
P2 (Encoding)	Mean	SD	N	P2 (Retrieval)	Mean	SD	N
LFZ	216,71	36,40	34	LFZ	205,42	37,67	34
LP3	236,44	25,83	34	LP3	239,89	35,18	34
LPZ	232,99	28,57	34	LPZ	228,35	39,75	35
LP4	240,81	22,30	34	LP4	243,57	32,78	34
LPO3	233,69	20,57	34	LPO3	242,88	26,74	34
LPO4	248,58	21,96	33	LPO4	250,76	24,49	31
LO1	236,17	22,54	34	LO1	237,05	27,52	35
LO2	242,19	18,65	34	LO2	248,44	24,76	35
AFZ	7,06	3,87	34	AFZ	6,70	4,58	34
AP3	6,95	3,51	34	AP3	4,43	4,20	34
APZ	7,09	3,38	34	APZ	5,16	4,67	35
AP4	7,75	4,05	34	AP4	5,38	4,04	34
APO3	5,72	4,11	34	APO3	3,27	4,33	34
APO4	6,22	4,85	33	APO4	4,26	5,26	31
AO1	6,35	3,71	34	AO1	4,02	3,83	35
AO2	7,29	4,46	34	AO2	4,82	4,51	35

Table A 5. Descriptives (absolute component appearance)

P1 to N1	"Alpha"
N1 to P2	"Theta"

	Mean	SD	N		Mean	SD	N
	ENCODING				**RETRIEVAL**		
FZ P1-N1	13,537	5,49	29	FZ P1-N1	15,128	5,72	33
FZ P1-P2	8,835	3,23	29	FZ P1-P2	9,880	3,11	32
FZ N1-P2	7,457	3,77	32	FZ N1-P2	8,147	3,12	32
P3 P1-N1	10,259	3,51	33	P3 P1-N1	**10,694**	6,12	32
P3 P1-P2	7,904	1,62	33	P3 P1-P2	7,883	2,31	32
P3 N1-P2	7,084	2,17	34	P3 N1-P2	7,375	2,72	32
PZ P1-N1	10,867	3,94	30	PZ P1-N1	**11,079**	6,03	31
PZ P1-P2	7,922	1,43	30	PZ P1-P2	8,416	3,22	31
PZ N1-P2	7,085	2,63	34	PZ N1-P2	7,881	3,41	33
P4 P1-N1	9,644	3,83	32	P4 P1-N1	8,753	3,70	32
P4 P1-P2	7,566	1,34	32	P4 P1-P2	7,606	2,05	32
P4 N1-P2	6,966	2,10	34	P4 N1-P2	7,642	3,08	33
PO3 P1-N1	9,867	3,42	33	PO3 P1-N1	9,109	3,54	33
PO3 P1-P2	8,124	1,42	33	PO3 P1-P2	7,756	1,59	32
PO3 N1-P2	7,485	1,82	34	PO3 N1-P2	7,778	2,66	32
PO4 P1-N1	9,169	3,41	30	PO4 P1-N1	9,050	3,52	32
PO4 P1-P2	7,411	1,22	30	PO4 P1-P2	7,768	1,97	29
PO4 N1-P2	6,807	1,95	33	PO4 N1-P2	7,419	2,37	29
O1 P1-N1	10,043	3,76	32	O1 P1-N1	10,053	4,02	31
O1 P1-P2	7,938	1,64	32	O1 P1-P2	8,196	1,94	31
O1 N1-P2	**6,905**	1,54	34	O1 N1-P2	7,912	2,32	33
O2 P1-N1	9,786	3,13	33	O2 P1-N1	8,751	2,87	33
O2 P1-P2	7,699	1,35	33	O2 P1-P2	7,394	1,54	33
O2 N1-P2	**6,804**	1,83	34	O2 N1-P2	7,063	2,17	33

Table A 6. Peak-to-Peak latencies (in frequencies)

Descriptive Statistics[a]

	Mean	Std. Deviation	N
IAFHZ	9.99	1.00	34
RECOG	46.26	6.70	34
IAFPOWER	11.766871	12.493165	33
FZP1TON1	13.5373837	5.4865435	29
PZP1TON1	10.8673016	3.9410922	30
P3P1TON1	10.2588482	3.5082915	33
P4P1TON1	9.8437951	3.8317147	32
PO3P1N1	9.8671214	3.4171923	33
PO4P1N1	9.1691775	3.4074950	30
O1P1TON1	10.0431692	3.7649386	32
O2P1TON1	9.7862434	3.1315922	33
FZN1TOP2	7.4574686	3.7660673	32
PZN1TOP2	7.0846888	2.6276136	34
P3N1TOP2	7.0639357	2.1659998	34
P4N1TOP2	6.9663774	2.0987096	34
PO3N1P2	7.4846278	1.8159383	34
PO4N1P2	6.8067555	1.9565750	33
O1N1TOP2	6.9049944	1.5435950	34
O2N1TOP2	6.8039793	1.8330740	34

a. LERNWIED = 0, COMP = P1

Correlations[a]

		IAFHZ	RECOG	IAFPOWER	FZP1TON1	PZP1TON1	P3P1TON1	P4P1TON1
IAFHZ	Pearson Correlation	1.000	.311*	-.256	.189	.012	.093	.279
	Sig. (1-tailed)		.037	.075	.163	.012	.304	.144
	N	34	34	33	29	30	33	32
RECOG	Pearson Correlation	.311*	1.000	-.036	.175	.134	.280	.144
	Sig. (1-tailed)	.037		.420	.182	.239	.057	.216
	N	34	34	34	29	30	33	32
IAFPOWER	Pearson Correlation	-.256	-.036	1.000	.080	-.131	.046	-.115
	Sig. (1-tailed)	.075	.420		.342	.250	.402	.265
	N	33	34	33	28	30	33	32
FZP1TON1	Pearson Correlation	.189	.175	.080	1.000	.089	-.026	.214
	Sig. (1-tailed)	.163	.182	.342		.330	.448	.137
	N	29	29	28	29	27	29	28
PZP1TON1	Pearson Correlation	.411*	.134	-.131	.089	1.000	.116	.137
	Sig. (1-tailed)	.012	.239	.250	.330		.271	.002
	N	28	30	30	27	30	30	28
P3P1TON1	Pearson Correlation	.093	.280	.046	-.026	.116	1.000	-.318*
	Sig. (1-tailed)	.304	.057	.402	.448	.271		.038
	N	33	33	33	29	30	33	32
P4P1TON1	Pearson Correlation	.279	.144	-.115	.214	.137	-.318*	1.000
	Sig. (1-tailed)	.144	.216	.265	.137	.002	.038	
	N	32	32	32	28	28	32	32
PO3P1N1	Pearson Correlation	-.052	.237	.034	-.292	.136	.679**	-.020
	Sig. (1-tailed)	.386	.092	.424	.066	.241	.000	.456
	N	33	33	32	28	29	32	32
PO4P1N1	Pearson Correlation	-.101	-.206	-.070	-.046	.034	.185	-.154
	Sig. (1-tailed)	.298	.138	.357	.412	.434	.169	.205
	N	30	32	30	26	27	29	32
O1P1TON1	Pearson Correlation	-.127	-.043	.049	-.278	.102	.499**	-.015
	Sig. (1-tailed)	.244	.408	.395	.076	.298	.002	.468
	N	32	32	32	28	29	32	31
O2P1TON1	Pearson Correlation	-.342*	-.287	-.108	-.219	-.066	.175	.290
	Sig. (1-tailed)	.026	.053	.274	.131	.366	.169	.054
	N	32	33	33	28	29	32	32
FZN1TOP2	Pearson Correlation	-.068	-.061	.234	-.028	.290	.077	.360*
	Sig. (1-tailed)	.356	.370	.103	.444	.063	.337	.025
	N	33	32	33	29	29	32	32
PZN1TOP2	Pearson Correlation	-.254	-.288*	-.013	.062	-.389*	.107	-.086
	Sig. (1-tailed)	.073	.049	.472	.375	.017	.277	.320
	N	34	34	33	29	30	33	32
P3N1TOP2	Pearson Correlation	-.005	-.408**	.135	.127	-.189	-.195	.059
	Sig. (1-tailed)	.488	.008	.227	.256	.159	.138	.374
	N	34	34	33	29	30	33	32
P4N1TOP2	Pearson Correlation	.056	-.320*	-.042	.227	-.305	-.080	-.196
	Sig. (1-tailed)	.376	.033	.407	.118	.050	.330	.141
	N	34	34	33	29	30	33	32
PO3N1P2	Pearson Correlation	.094	-.386*	.198	.127	-.098	-.178	.060
	Sig. (1-tailed)	.298	.012	.134	.256	.304	.161	.371
	N	34	34	33	29	30	33	32
PO4N1P2	Pearson Correlation	.020	-.127	.291	-.085	-.224	-.318*	-.154
	Sig. (1-tailed)	.455	.241	.053	.334	.164	.038	.205
	N	33	33	32	28	29	32	32
O1N1TOP2	Pearson Correlation	.080	-.054	.158	.143	-.224	.093	-.020
	Sig. (1-tailed)	.327	.380	.190	.230	.117	.303	.456
	N	34	34	33	29	30	33	32
O2N1TOP2	Pearson Correlation	.049	.026	.178	.168	-.014	-.091	-.271
	Sig. (1-tailed)	.391	.441	.161	.192	.470	.307	.067
	N	34	34	33	29	30	33	32

Table A 7. Correlation matrix for peak-to-peak latencies (encoding)

Retrieval Peak-to-peak Latency Correlations

Descriptive Statistics[a]

	Mean	Std. Deviation	N
IAFHZ	10.04	1.00	35
RECOG	46.11	6.57	35
IAFPOWER	11.306485	12.307852	34
WFZP1N1	14.8904759	5.6491899	35
WPZP1N1	11.0537274	5.8395526	33
WO1P1N1	9.8154398	4.0369142	33
WO2P1N1	8.9367800	3.0486943	35
WP3P1N1	5.9931840		34
WP4P1N1	8.7298614	3.6411720	33
WPO3P1N1	9.2155514	3.4947112	35
WPO4P1N1	9.0667555	3.4257580	34
WFZN1P2	7.9454096	3.1572267	34
WPZN1P2	7.6299385	3.4669267	35
WP3N1P2	7.2806961	2.7228829	34
WP4N1P2	7.5215686	3.1173656	34
WPO3N1P2	7.5999636	2.6849316	34
WPO4N1P2	7.2842799	2.3954535	31
WO1N1P2	7.8285446	2.3726182	35
WO2N1P2	6.9771388	2.1669318	35

a. LERNWIED = 1; COMP = P1

Correlations[a]

		IAFHZ	RECOG	IAFPOWER	WFZP1N1	WPZP1N1	WO1P1N1	WO2P1N1
IAFHZ	Pearson Correlation	1.000	.224	-.263	.372*	-.188	-.340*	-.311*
	Sig. (1-tailed)	.	.097	.066	.014	.147	.026	.034
	N	35	35	34	34	33	33	35
RECOG	Pearson Correlation	.224	1.000	.030	.287*	-.201	.087	-.279
	Sig. (1-tailed)	.097	.	.434	.047	.132	.316	.052
	N	35	35	34	35	33	33	35
IAFPOWER	Pearson Correlation	-.263	.030	1.000	.108	.022	.209	.042
	Sig. (1-tailed)	.066	.434	.	.271	.452	.125	.408
	N	34	34	34	34	33	32	34
WFZP1N1	Pearson Correlation	.372*	.287*	.108	1.000	-.012	-.124	-.240
	Sig. (1-tailed)	.014	.047	.271	.	.473	.246	.083
	N	34	35	34	35	33	33	34
WO1P1N1	Pearson Correlation	-.340*	.087	.209	-.124	.367*	1.000	.877**
	Sig. (1-tailed)	.026	.316	.125	.246	.019	.	.000
	N	33	33	32	33	32	33	33
WFZN1P2	Pearson Correlation	-.340*	.067	.125	.019	.367*	.529**	.001
	Sig. (1-tailed)	.026	.316	.125	.019	.019	.000	.006
	N	34	33	32	33	33	31	33
WPO4P1N1	Pearson Correlation	-.043	.094	.206	.110	-.059	.005	.110
	Sig. (1-tailed)	.408	.308	.137	.277	.379	.489	.277
	N	34	34	33	34	32	32	34
WPO3P1N1	Pearson Correlation	.051	.108	-.136	.057	-.022	-.019	.167
	Sig. (1-tailed)	.386	.271	.226	.374	.452	.459	.172
	N	34	34	33	34	32	32	34
WP4P1N1	Pearson Correlation	.048	.082	-.193	-.081	.453**	.336*	.218
	Sig. (1-tailed)	.396	.326	.145	.328	.005	.032	.112
	N	34	34	32	34	31	32	33
WP3P1N1	Pearson Correlation	-.120	-.166	.071	.245	.842**	.318*	.086
	Sig. (1-tailed)	.249	.174	.347	.081	.000	.038	.313
	N	34	34	33	34	33	32	34
WO2P1N1	Pearson Correlation	-.311*	-.279	.042	-.240	.403**	.677**	1.000
	Sig. (1-tailed)	.034	.052	.408	.083	.010	.000	.
	N	35	35	34	34	33	33	35
WP2N1P2	Pearson Correlation	-.020	-.029	-.104	-.119	.223	.064	-.014
	Sig. (1-tailed)	.454	.435	.279	.247	.107	.361	.469
	N	35	35	34	34	32	32	35
WPO4N1P2	Pearson Correlation	-.293*	-.188	.259	-.016	.311*	.452**	.452**
	Sig. (1-tailed)	.046	.144	.073	.465	.041	.005	.004
	N	35	34	34	35	33	33	35
WPO3N1P2	Pearson Correlation	-.131	-.158	.143	-.037	.266	.529**	.006
	Sig. (1-tailed)	.227	.183	.073	.337		.001	
	N	33	33	33	33	31	31	33
WP4N1P2	Pearson Correlation	-.340*	.087	.209	-.124	.367*	.336*	.877**
	Sig. (1-tailed)	.026	.316	.125	.246	.019	.032	
	N	33	33	32	33	32	32	33
WP3N1P2	Pearson Correlation	-.188	-.201	.022	-.012	1.000	.367*	.403**
	Sig. (1-tailed)	.147	.132	.452	.473	.	.019	.010
	N	33	33	33	33	33	32	35
WO1N1P2	Pearson Correlation	.039	.117	.013	.102	-.160	.005	-.215
	Sig. (1-tailed)	.412	.251	.470	.280	.187	.137	.108
	N	35	35	34	35	33	33	35
WO2N1P2	Pearson Correlation	.100	.132	.183	.066	-.111	-.132	-.155
	Sig. (1-tailed)	.283	.224	.150	.311	.270	.232	.187
	N	35	35	34	35	33	33	35

Table A 8. Correlation matrix for peak-to-peak latencies (retrieval)

Encoding Peak-to-Peak Amplitude Correlations

Descriptive Statistics[a]

	Mean	Std. Deviation	N
IAFHZ	9.99	1.00	34
RECOG	46.26	6.70	34
IAFPOWER	11.766871	12.493165	33
PLFZP1N1	4.1134041	2.4122239	29
PLFZP2N1	6.3388900	4.3774048	30
PLP3P1N1	8.0300399	4.4912652	33
PLP4P1N1	8.4998954	4.6071626	32
PLPO3P1N1	9.0836173	4.6074993	33
PLPO4P1N1	8.7209852	4.0312021	30
PLO1P1N1	8.4383837	4.9849124	32
PLO2P1N1	8.2833901	4.3648793	33
PLFZP2N1	9.5723564	4.7105296	32
PLP3P2N1	12.1821456	5.5447390	34
PLP4P2N1	12.6841178	5.5883437	34
PLPO3P2N1	14.0355877	6.1030587	34
PLPO4P2N1	11.9697434	5.7374345	34
PLO1P2N1	12.3069844	6.6560201	33
PLO2P2N1	12.3444973	5.3203449	34
PLO2P2N1	13.5012872	8.5003297	34

a. LERNWIED = 0, COMP = P1

Correlations[a]

	IAFHZ	RECOG	IAFPOWER	PLFZP1N1	PLFZP2N1	PLP3P1N1	PLP4P1N1
IAFHZ Pearson Correlation	1,000	,311*	-,256	-,085	-,145	,049	-,105
Sig. (1-tailed)		,037	,075	,331	,222	,394	,284
N	34	34	33	29	30	33	32
RECOG Pearson Correlation	,311*	1,000	-,006	-,336*	,222	,394	-,244
Sig. (1-tailed)	,037		,420	,037	,004	,085	,047
N	34	34	33	33	30	33	32
IAFPOWER Pearson Correlation	-,256	-,036	1,000	,093	,125	-,098	-,034
Sig. (1-tailed)	,075	,420		,319	,259	,298	,426
N	33	33	33	28	29	32	32
PLFZP1N1 Pearson Correlation	-,085	-,336*	,093	1,000	,633**	,528**	,244
Sig. (1-tailed)	,331	,037	,319		,000	,001	,105
N	29	33	28	29	27	29	32
PLPO3P1N1 Pearson Correlation	,176	,040	,163	,218	,234	,606**	,522**
Sig. (1-tailed)	,164	,412	,182	,132	,111	,000	,001
N	33	33	32	28	29	32	32
PLPO4P1N1 Pearson Correlation	,009	-,076	,123	,062	,222	,444**	,690**
Sig. (1-tailed)	,461	,344	,259	,381	,133	,008	,000
N	30	30	30	26	27	29	32
PLO1P1N1 Pearson Correlation	,398*	-,049	-,064	,079	,107	,515*	,414*
Sig. (1-tailed)	,012	,394	,364	,345	,290	,001	,010
N	32	32	32	28	29	32	31
PLO2P1N1 Pearson Correlation	,253	,013	-,220	,131	,158	,537**	,620**
Sig. (1-tailed)	,078	,471	,109	,253	,206	,001	,000
N	33	33	32	28	29	32	32
PLFZP2N1 Pearson Correlation	-,065	,013	-,060	,426*	,176	,350*	,117
Sig. (1-tailed)	,362	,473	,374	,011	,181	,025	,270
N	32	32	31	29	29	32	30
PLP4P2N1 Pearson Correlation	-,105	-,301*	-,034	,244	,000	,885**	1,000
Sig. (1-tailed)	,284	,047	,426	,105	,000	,000	
N	33	33	32	28	29	30	31
PLP3P1N1 Pearson Correlation	,049	-,244	-,098	,536**	,703**	1,000	,685**
Sig. (1-tailed)	,394	,085	,298	,001	,000		,000
N	33	33	32	29	30	34	29
PLP2P1N1 Pearson Correlation	-,145	-,473**	,125	,633**	1,000	,703**	,611**
Sig. (1-tailed)	,222	,004	,259	,000		,000	,000
N	30	30	29	29	27	30	28
PLP9P2N1 Pearson Correlation	,009	,105	,110	,408*	,337*	,528**	,333*
Sig. (1-tailed)	,479	,277	,272	,014	,034	,001	,031
N	34	34	33	29	30	33	32
PLP2P2N1 Pearson Correlation	-,037	,066	,121	,555**	,488**	,524**	,241
Sig. (1-tailed)	,419	,355	,250	,001	,003	,001	,092
N	34	34	33	29	30	33	30
PLP4P2N1 Pearson Correlation	,077	-,068	,083	,025	,324*	,411**	,484**
Sig. (1-tailed)	,333	,351	,322	,449	,040	,009	,003
N	34	34	33	29	30	33	32
PLPO3P2N1 Pearson Correlation	,161	,222	,209	,102	-,107	,203	,012
Sig. (1-tailed)	,181	,103	,122	,300	,287	,129	,474
N	34	34	33	29	30	33	32
PLPO4P2N1 Pearson Correlation	,174	,043	,225	-,085	-,027	,161	,067
Sig. (1-tailed)	,167	,406	,108	,333	,444	,189	,360
N	34	34	32	28	29	33	32
PLO1P2N1 Pearson Correlation	,326*	,244	,160	-,018	-,201	,089	-,059
Sig. (1-tailed)	,030	,082	,187	,464	,144	,312	,375
N	33	34	33	29	29	33	31
PLO2P2N1 Pearson Correlation	,188	,026	,130	-,031	-,028	,206	,092
Sig. (1-tailed)	,143	,443	,235	,437	,442	,125	,309
N	34	34	33	29	30	33	32

Table A 9. Correlation matrix for peak-to-peak amplitudes (encoding)

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Retrieval Peak-to-Peak Amplitude Correlations

Descriptive Statistics[a]

	Mean	Std. Deviation	N
IAFHZ	10,04	1,00	35
RECOG	46,11	6,57	35
IAFPOWER	11,306485	12,307852	34
PWFZP1N1	3,7241610	2,2074222	34
PWPZP1N1	5,5642492	3,0556973	33
PWP3P1N1	8,2491390	5,1576460	34
PWP4P1N1	9,7933762	5,6734688	33
PWPO3PN1	10,6970488	5,5884957	35
PWPO4PN1	10,6903351	5,7923054	34
PWO1P1N1	10,7098625	6,2528931	33
PWO2P1N1	10,2208794	5,5499840	35
PWFZP2N1	10,4335999	6,0633586	34
PWP2P2N1	11,8299114	6,6796993	35
PWP3P2N1	12,4228863	6,6434690	34
PWP4P2N1	13,4079683	6,4489550	33
PWPO3P2N	11,9051464	7,2456607	34
PWPO4P2N	11,4863788	6,6912033	31
PWO1P2N1	11,8078294	6,4929358	35
PWO2P2N1	12,3091675	6,8134572	35

a. LERNWIED = 1, COMP = P1

Correlations[a]

		IAFHZ	RECOG	IAFPOWER	PWFZP1N1	PWPZP1N1	PWP3P1N1	PWP4P1N1
IAFHZ	Pearson Correlation	1,000	,224	-,263	-,113	-,002	,055	-,106
	Sig. (1-tailed)		,097	,066	,258	,496	,379	,278
	N	35	35	34	34	33	34	33
RECOG	Pearson Correlation	,224	1,000	,030	-,393**	,258	,086	-,157
	Sig. (1-tailed)	,097		,434	,010	,496	,315	,191
	N	35	35	34	34	33	34	33
IAFPOWER	Pearson Correlation	-,263	,030	1,000	-,042	-,085	,288	,014
	Sig. (1-tailed)	,066	,434		,408	,321	,052	,471
	N	34	34	34	34	32	33	32
PWFZP1N1	Pearson Correlation	-,113	-,393**	-,042	1,000	,479**	,158	,396*
	Sig. (1-tailed)	,258	,010	,408		,002	,186	,028
	N	34	34	34	34	33	33	32
PWPZP1N1	Pearson Correlation	-,002	,010	-,085	,479**	1,000	,600**	,683**
	Sig. (1-tailed)	,496	,408	,321	,002		,000	,000
	N	33	33	32	33	33	32	31
PWP3P1N1	Pearson Correlation	,055	,086	,288	,158	,600**	1,000	,597**
	Sig. (1-tailed)	,379	,315	,052	,186	,000		,000
	N	34	34	33	33	32	34	32
PWP4P1N1	Pearson Correlation	-,106	-,157	,014	,396*	,683**	,597**	1,000
	Sig. (1-tailed)	,278	,191	,471	,028	,000	,000	
	N	33	33	32	32	31	32	33
PWPO3PN1	Pearson Correlation	,191	,154	,030	,080	,402**	,693**	,532**
	Sig. (1-tailed)	,136	,189	,433	,323	,010	,000	,001
	N	33	35	34	35	33	32	33
PWPO4PN1	Pearson Correlation	,019	-,008	,231	,284	,399**	,432**	,883**
	Sig. (1-tailed)	,457	,483	,098	,052	,012	,006	,000
	N	34	34	33	35	33	34	33
PWO1P1N1	Pearson Correlation	,321*	,125	-,118	,176	,422**	,580**	,475**
	Sig. (1-tailed)	,034	,243	,260	,192	,006	,000	,003
	N	34	33	32	34	32	33	32
PWFZP2N1	Pearson Correlation	,040	,064	-,015	,154	,103	,045	-,028
	Sig. (1-tailed)	,412	,360	,466	,287	,402	,209	,095
	N	34	34	34	35	33	34	33
PWP2P2N1	Pearson Correlation	-,019	-,096	,021	,149	,439**	,209	,234
	Sig. (1-tailed)	,456	,293	,452	,196	,005	,118	,095
	N	35	34	33	34	32	33	33
PWP3P2N1	Pearson Correlation	,024	-,018	-,011	,075	,468**	,491**	,290
	Sig. (1-tailed)	,446	,460	,476	,202	,003	,002	,054
	N	34	35	34	35	32	34	33
PWP4P2N1	Pearson Correlation	-,050	-,150	,112	,202	,614**	,340*	,662**
	Sig. (1-tailed)	,392	,203	,271	,129	,000	,028	,000
	N	34	34	32	34	32	34	32
PWPO3P2N	Pearson Correlation	,088	-,038	,192	,144	,383*	,325*	,233
	Sig. (1-tailed)	,310	,415	,142	,209	,015	,032	,100
	N	33	33	32	34	32	33	32
PWPO4P2N	Pearson Correlation	,164	-,076	,280	,208	,384*	,137	,476**
	Sig. (1-tailed)	,190	,343	,067	,131	,018	,235	,005
	N	34	30	30	31	30	30	29
PWO1P2N1	Pearson Correlation	,189	-,012	,218	,161	,013	,217	,239
	Sig. (1-tailed)	,138	,472	,108	,178	,472	,108	,090
	N	35	35	34	35	30	34	33
PWO2P2N1	Pearson Correlation	,127	-,102	,155	,212	,441**	,219	,366*
	Sig. (1-tailed)	,234	,281	,191	,111	,005	,107	,018
	N	35	35	34	35	33	34	33

Table A 10. Correlation matrix for peak-to-peak amplitudes (retrieval)

Figure A 2. ERP Total vs. Alpha ERP (Encoding)

Exact ERP-latencies and amplitudes for ERP-Total O1, ERP-Total O2, Alpha ERP O1 and Alpha ERP O2 as follows: P1 (105ms / 0.7µV , 100ms / 0.5µV, 110ms / 2.1µV, 110ms / 2.1µV), N1 (165ms / -4.6µV, 165ms / -5µV, 170ms / -2.5µV, 170ms / -2.5µV) and P2 (240ms / 5.7µV, 240ms / 6.1µV, 228ms / 2µV, 228ms / 2µV).
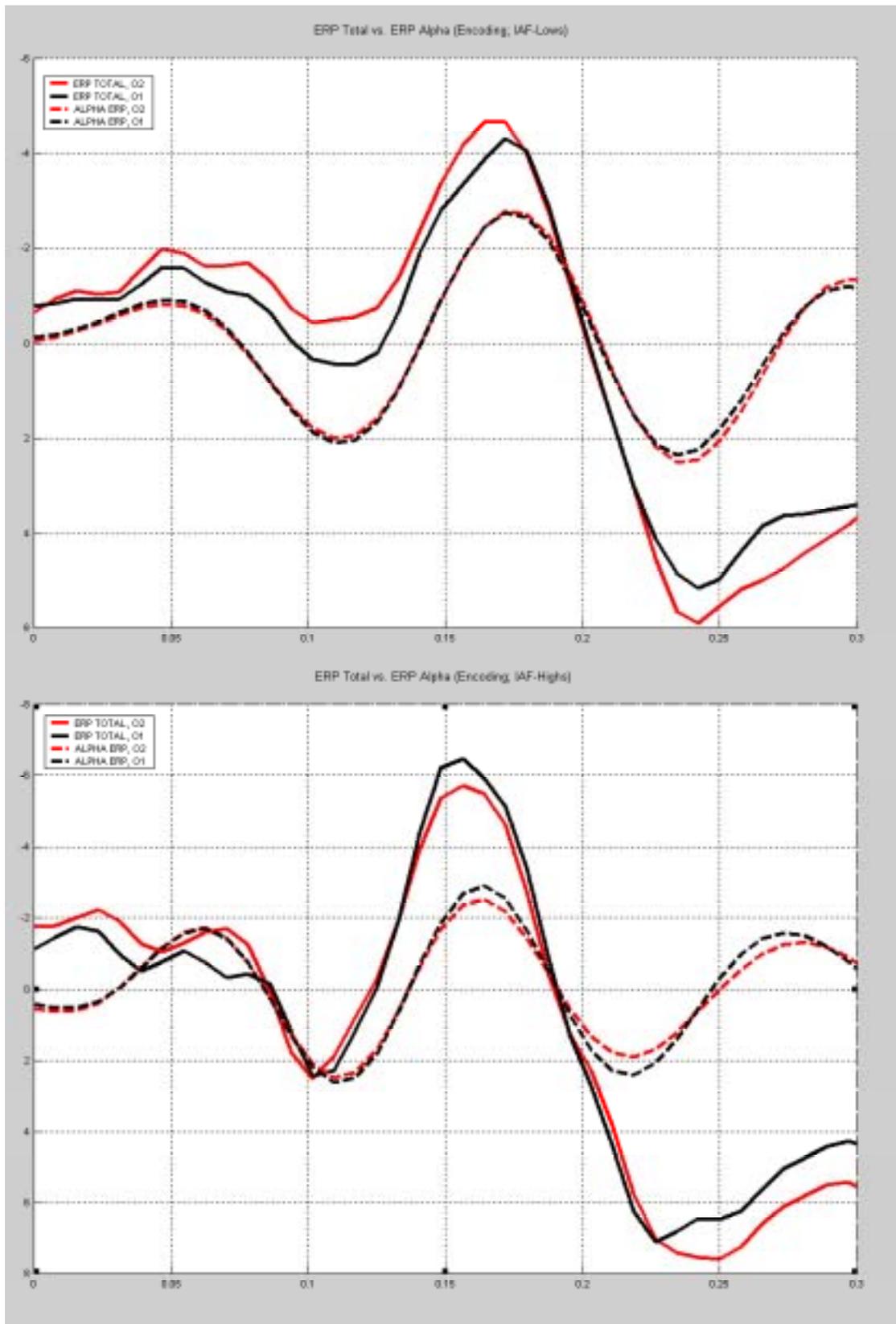
Figure A 3. ERP Total vs. Alpha ERP during encoding for IAF-Lows and IAF-Highs

Exact ERP-latencies and amplitudes for ERP-Total O1, ERP-Total O2, Alpha ERP O1 and Alpha ERP O2 as follows for IAF-Lows Encoding (upper graph): P1 (115ms / 0.5µV , 105ms / -0.5µV, 110ms / 2.1µV, 110ms / 2µV), N1 (172ms / -4.3µV, 166ms / -4.7µV, 172ms / -2.8µV, 172ms / -2.8µV) and P2 (241ms / 5.1µV, 241ms / 5.9µV, 235ms / 2.3µV, 235ms / 2.5µV); and IAF-Highs Encoding (lower): P1 (100ms / 2.5µV , 100ms / 2.5µV, 110ms / 2.6µV, 110ms / 2.6µV), N1 (155ms / -6.5µV, 155ms / -5.7µV, 165ms / -2.9µV, 165ms / -2.5µV) and P2 (226ms / 7.1µV, 245ms / 7.6µV, 220ms / 2.4µV, 220ms / 1.9µV).

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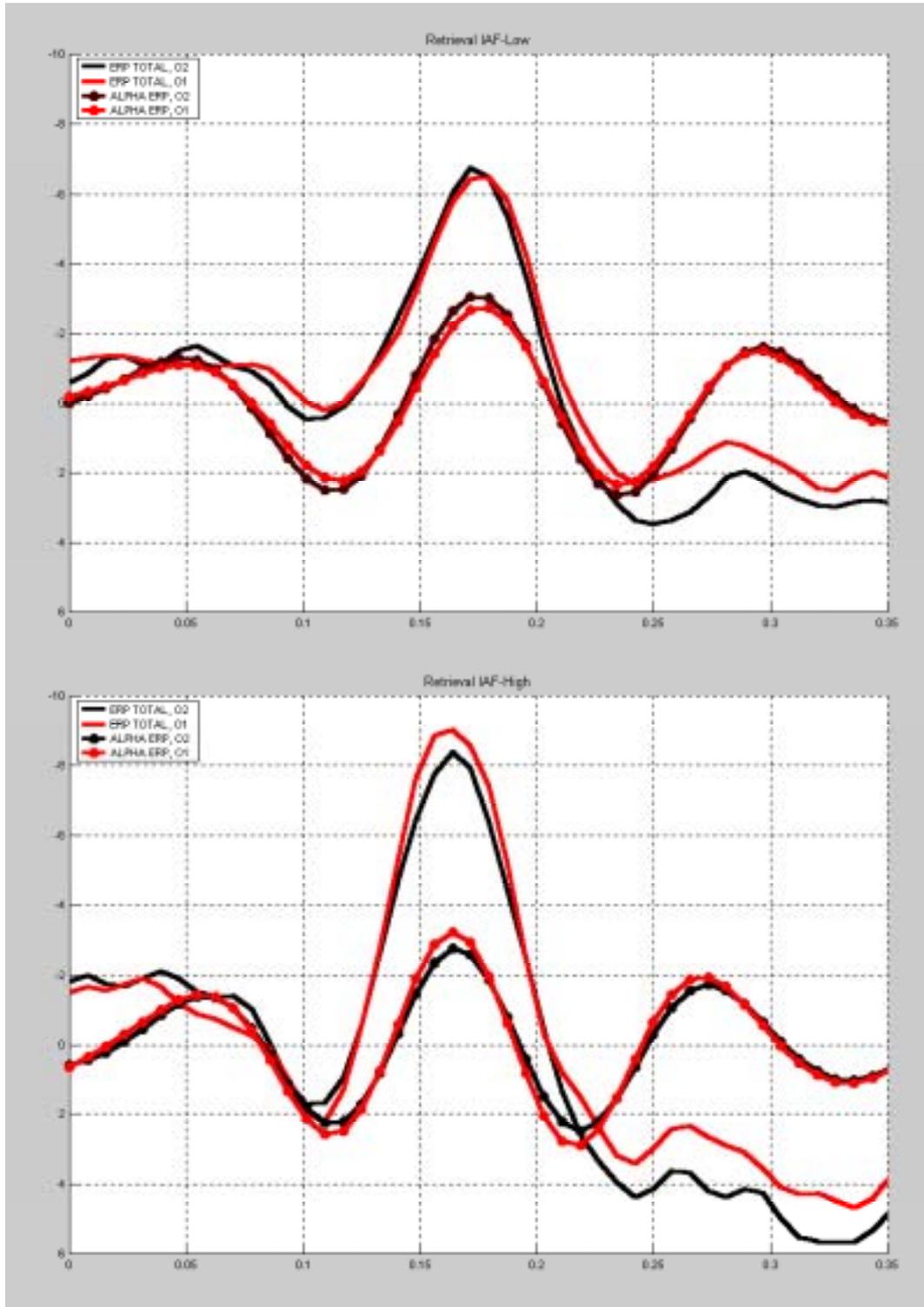
Figure A 4. ERP Total vs. Alpha ERP during retrieval for IAF-Lows and IAF-Highs

Exact ERP-latencies and amplitudes for ERP-Total O1, ERP-Total O2, Alpha ERP O1 and Alpha ERP O2 as follows for IAF-Lows Retrieval (upper graph): P1 (110ms / 0.1µV , 100ms / 0.5µV, 118ms / 2.2µV, 113ms / 2.5µV), N1 (180ms / -6.5µV, 171ms / -6.8µV, 175ms / -2.7µV, 175ms / -3µV) and P2 (242ms / 2.3µV, 250ms / 3.5µV, 235ms / 2.4µV, 234ms / 2.7µV); and IAF-Highs Retrieval (lower): P1 (110ms / 2.2µV , 102ms / 1.7µV, 110ms / 2.6µV, 110ms / 2.2µV), N1 (165ms / -9µV, 165ms / -8.4µV, 164ms / -3.2µV, 164ms / -2.7µV) and P2 (242ms / 3.5µV, 242ms / 4.4µV, 219ms / 2.9µV, 219ms / 2.5µV).
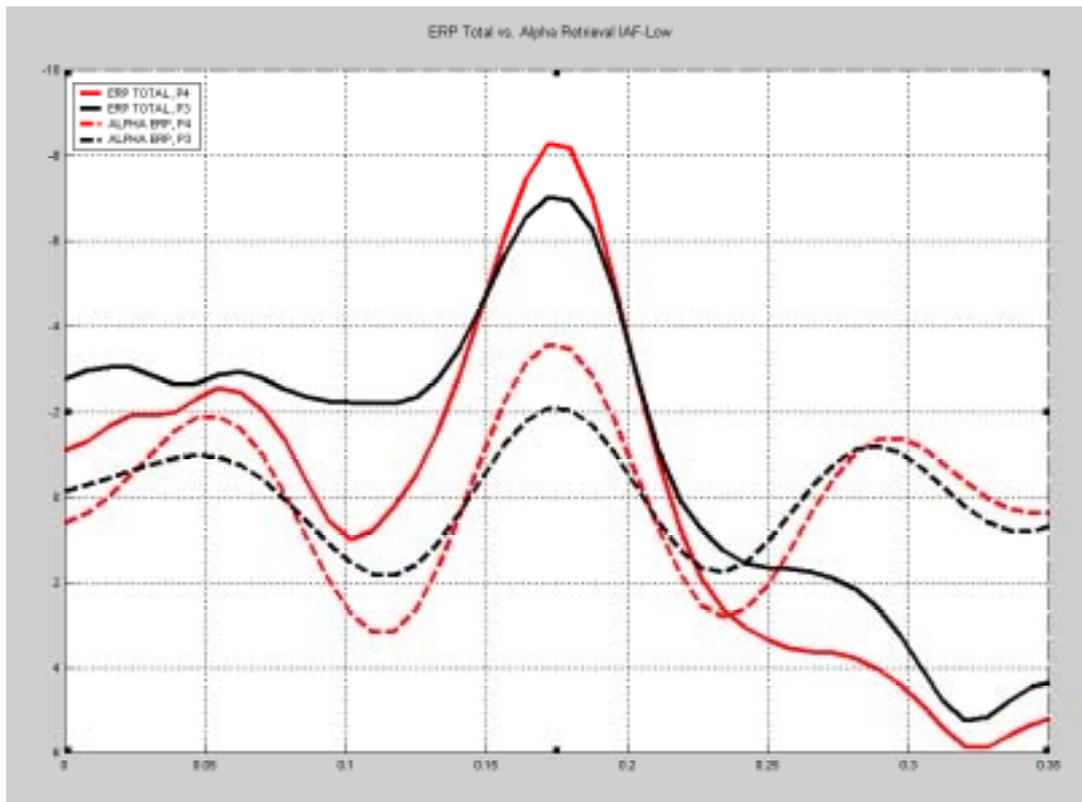
Figure A 5. ERP Total vs. Alpha ERP during retrieval (IAF-Lows)

Note the strong interdependent course of the respective standard ERP with the corresponding alpha ERP.
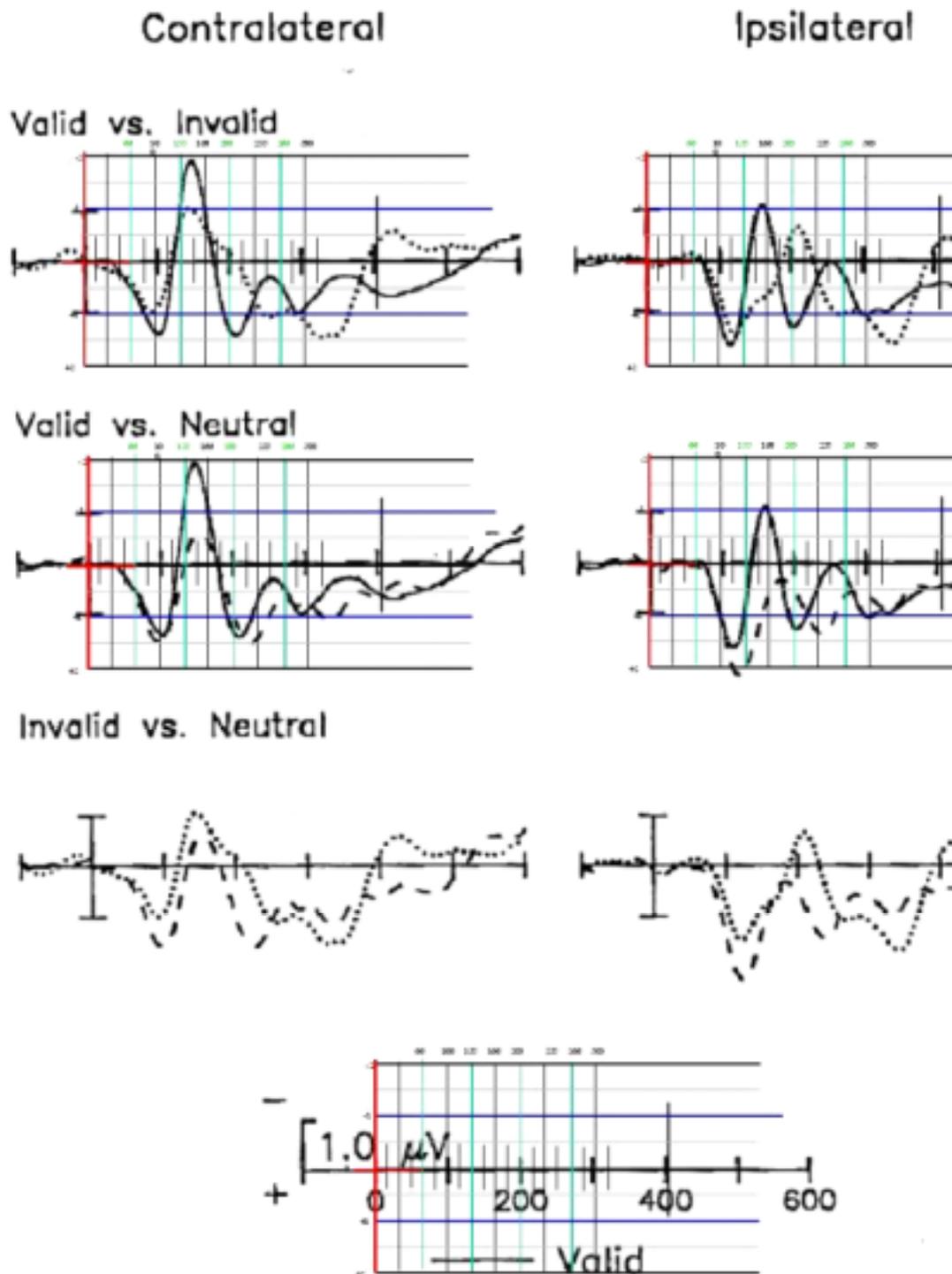
Figure A 6. Example of an ERP-figure measured with templates

The figure was first zoomed then scanned and finally the peaks were measured using a "scale-template" (colored). Data from: Hillyard, Luck, & Mangun (1994).

10 <u>Figure Caption</u>

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