



# Memory processes, brain oscillations and EEG synchronization

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Received 16 February 1996; revised 1 June 1996; accepted 19 August 1996

## Abstract

This article tries to integrate results in memory research from divergent disciplines such as cognitive psychology, neuroanatomy, and neurophysiology. The integrating link is seen in more recent findings that provide strong arguments for the 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. On the other hand, during mental activity, when different neuronal networks may start to oscillate with different frequencies, each network may still oscillate synchronously (this is termed type 2 synchronization), but as a consequence, the large scale type 1 oscillation disappears. It is argued that these different types of synchronization can be observed in the scalp EEG by calculating event-related power changes within comparatively narrow but individually adjusted frequency bands. Experimental findings are discussed which support the hypothesis that short-term (episodic) memory demands lead to a synchronization (increase in band power) in the theta band, whereas long-term (semantic) memory demands lead to a task-specific desynchronization (decrease or suppression of power) in the upper alpha band. Based on these and other findings, a new memory model is proposed that is described on three levels: cognitive, anatomical and neurophysiological. It is suggested that short-term (episodic) memory processes are reflected by oscillations in an anterior limbic system, whereas long-term (semantic) memory processes are reflected by oscillations in a posterior-thalamic system. Oscillations in these frequency bands possibly provide the basis for encoding, accessing, and retrieving cortical codes that are stored in the form of widely distributed but intensely interconnected cell assemblies.

**Keywords:** Memory; Oscillation; EEG; Theta band; Alpha band; Hippocampus; Thalamus

## 1. Introduction

Any memory theory is confronted by the representational problem, i.e. the question of how information is stored in memory. Representational assumptions can be made on an abstract or concrete level. As an example, abstract representational as-

sumptions typically refer to the distinction between different types of memory such as short-term (STM) or long-term memory (LTM) or episodic and semantic memory (Tulving, 1984). Network and spreading activation models (e.g., Anderson's well known ACT\* model; Anderson, 1983) are examples of theories relying on more concrete representational assumptions. Finally, as we all know, any memory process is a process occurring in our brains. More recently, several attempts have been made, to link

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the more abstract level of cognitive psychology with the more specific neurobiological or neurophysiological level (e.g., Posner, 1995, Tulving, 1995). But even within the rather specific biological approach there are relatively more abstract representational assumptions, referring, for example, to the question of which parts of the brain are involved in retrieval or storage of information. One of the most explicit and concrete levels which can be achieved in explaining memory processes and cognitive processes in general is the neuronal level.

While keeping in mind that any type of representational assumption has to refer to the structural and the processing aspects of representation, we also have to consider this distinction at the neuronal level. Structural assumptions refer to the type of connectivity between neurons, processing assumptions to the electrophysiological properties of signal processing. Given the fact that the transmission of information in the brain is based on electrophysiological processes (which are mediated and modified by biochemical processes), the neuronal-electrophysiological level is the most specific and explicit level of representational assumptions that can be reached.

It is the aim of the present paper to link cognitive psychology to neurophysiological findings and to provide evidence for a model that explains memory processes on the basis of electrophysiological processes. The processing assumptions of the proposed model are based on empirical findings and arguments which demonstrate that brain oscillations represent a basic form of information transmission in the brain. Brain oscillations will be primarily described in terms of synchronization, desynchronization and frequency shifts. The structural assumptions refer to specific properties of neuronal interconnectivity. Thus, the proposed model tries to explain memory processes in terms of different types of brain oscillations that can be observed in particular regions of the brain. According to the basic assumption that brain oscillations or brain rhythms are essential for memory processes, it is obvious to consider first empirical findings which refer to the alpha rhythm as the most dominant brain oscillation in the human EEG. Thus, it is important to provide some basic insight into the possible physiological meaning of synchronization, desynchronization and frequency shifts of brain oscillations.

## 2. EEG alpha and memory

The research reported in this section was prompted by a new memory theory, the 'connectivity model' (Klimesch, 1987, Klimesch, 1994). The central prediction of this theory which was supported by a series of experiments (see for example, the summary in Klimesch, 1994) is that increasing memory performance is related to increasing processing speed. Based on this 'memory speed effect' and on arguments that are discussed in later sections of this paper, the hypothesis was tested that the frequency of the alpha rhythm is related to memory performance.

A critical evaluation of the proposed hypothesis requires an understanding of the basic properties of the alpha rhythm, which first was described by Berger in the late 1920s and early 1930s (e.g., Berger, 1929). One of these basic properties refer to the fact that alpha desynchronizes or becomes suppressed during mental activity.

### 2.1. Alpha synchronization and desynchronization

According to Niedermeyer (1987), the most important criteria for defining the EEG alpha rhythm are: Alpha is (i) a rhythm with a frequency of about 8–13 Hz (ii) occurs during wakefulness over the posterior regions of the head, (iii) it is best seen with eyes closed and under conditions of physical relaxation and mental inactivity, (iv) it is blocked or attenuated by attention, and mental effort. Fig. 1 shows a typical example of an alpha rhythm recorded during an experimental session in one of our experimental studies. The subjects task was to judge whether the presented word represents an animal. The presentation of a word is preceded by a warning signal. As Fig. 1 shows, during the first sec. in which the subject is assumed to be in a state of relative mental inactivity, a pronounced rhythmic EEG activity — the alpha rhythm — can be observed. This interval is termed 'reference interval'. Note that the amplitudes of the alpha rhythm are more pronounced over occipital and parietal than over frontal and central recording sites. Even before the warning signal appears (the subject runs through many trials and thus anticipates the warning signal), the alpha rhythm begins to disappear. Only with the help of

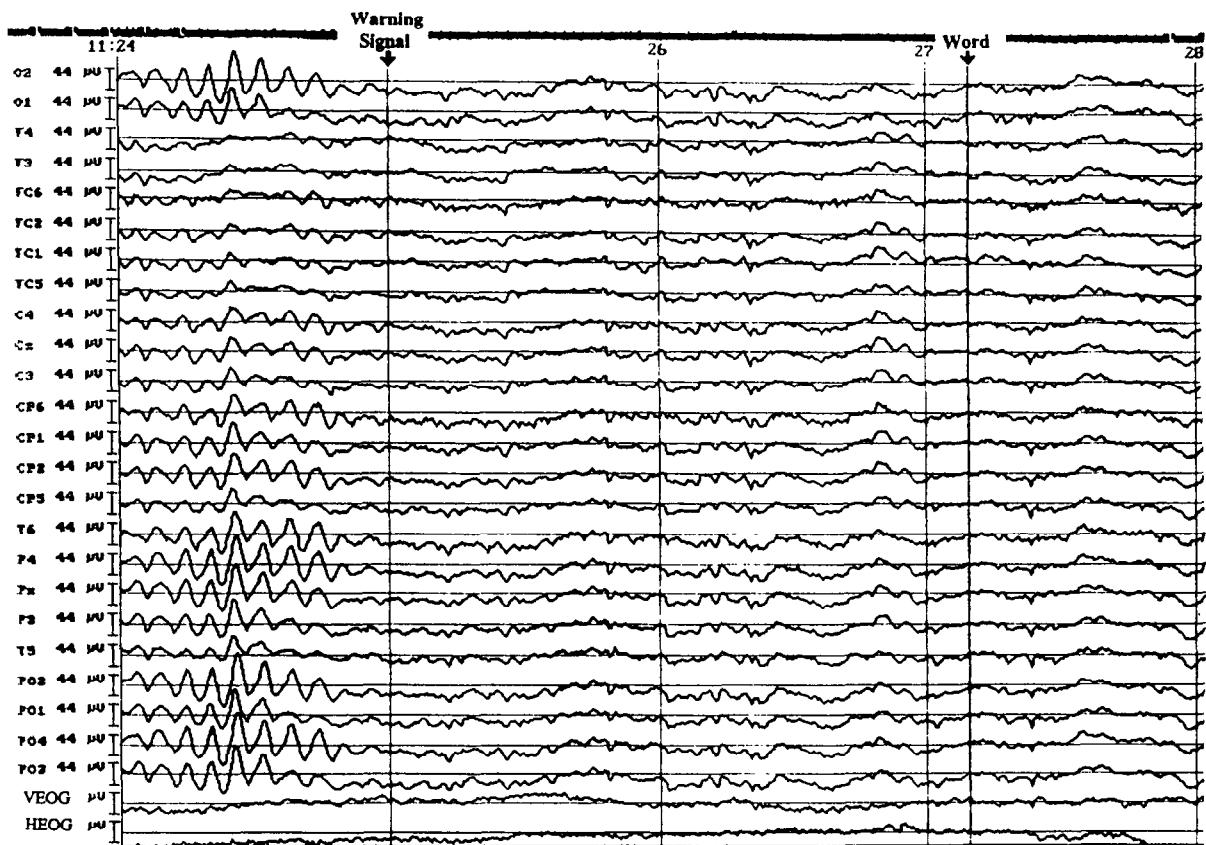


Fig. 1. Typical example of an EEG epoch, showing the basic principle of EEG synchronization and desynchronization. Each horizontal line represents a different recording site. Vertical lines mark time intervals of 1 s. During the first second, which is called reference interval, the subject shows pronounced rhythmic alpha activity. This indicates that very large cell assemblies are oscillating with the same phase and within a narrow frequency window. Because each subject runs through many trials, the increased alertness reflecting the anticipation of the warning signal already causes alpha to desynchronize even before the warning signal actually appears. As spectral analysis shows, this attentional effect is reflected only in the lower alpha band (see Fig. 7). The time intervals following the reference interval are called test intervals.

spectral analysis it is possible to monitor the behavior of the alpha rhythm during the time it is suppressed (blocked or desynchronized). The time period in which a subject is performing or preparing for a task is termed the test interval. Examples of power spectra showing the reference interval (with pronounced alpha peak) and the test interval (alpha power suppression) for frontal, parietal and occipital recording sites are shown in Fig. 2.

The fact that a dominant rhythm like alpha can be recorded with scalp electrodes documents the simple but important fact that below that recording site a very large population of neurons oscillates synchronously with the same phase and with the same

frequency or at least within a narrow frequency window. This type of 'large scale' synchronous oscillation is termed 'type 1 oscillation'. The interesting question now is which processes underly desynchronization (we use the term desynchronization synonymously with suppression or blocking).

Because there is strong evidence for the view that there is no single alpha rhythm but instead a population of different alpha rhythms (e.g., Grey Walter in Evans and Mulholland, 1969, p. 115; Lopes da Silva et al., 1973, Lopes Da Silva et al., 1980, and Basar and Bullock, 1992 for a more recent review) it seems quite obvious to assume that during desynchronization different alpha rhythms start to oscillate with

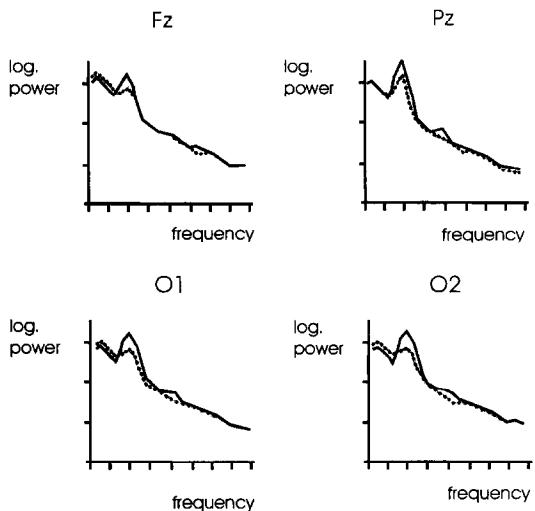


Fig. 2. Examples of power spectra reflecting the reference and test interval for selected recording sites. The large peak reflects alpha power during the reference (bold lines), the smaller peak reflects the test interval (dotted lines).

different frequencies. As a result, the dominant EEG alpha rhythm starts to desynchronize. This idea that in response to a cognitive demand, different alpha subpopulations begin to shift (either increase or decrease) their frequencies is depicted in Fig. 3. It is important to note that although the entire population of alpha rhythms reflects a process of desynchronization, each subpopulation may still oscillate synchronously. This latter type of micro scale synchronous oscillation is termed 'type 2 oscillation'.

## 2.2. The measurement of alpha synchronization and desynchronization

Pfurtscheller and Aranibar (1977) were the first to define a measure for alpha desynchronization and synchronization, coining the term event-related desynchronization (ERD). 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 time period within a single trial (epoch) preceding the presentation of a warning signal (cf. Fig. 1). Any time period, following the reference interval can be used as test interval. Thus, with a series of test intervals, the time course of shifts in band power can be monitored over the entire trial. The method of processing single epochs

was described in detail elsewhere (e.g., Pfurtscheller and Klimesch, 1991, Pfurtscheller and Klimesch, 1992a) but for a basic understanding, the most important steps of the procedure will be briefly outlined. First, artefact free EEG epochs are digitally band pass filtered within a defined frequency band. Second, in order to get a simple measure of band power, each sample point (i.e., band pass filtered EEG amplitude) of each epoch is squared. Third, these data are averaged separately over epochs and electrodes and after selecting the reference interval, the remaining part of the averaged epoch is segmented in a series of test intervals. Time resolution is limited by the length of the test intervals which can be as small as 125 ms. As an example, if sampling frequency is 128 Hz and test intervals have a length of 125 ms, each test interval represents the

— reference  
..... test, easy  
... test, difficult

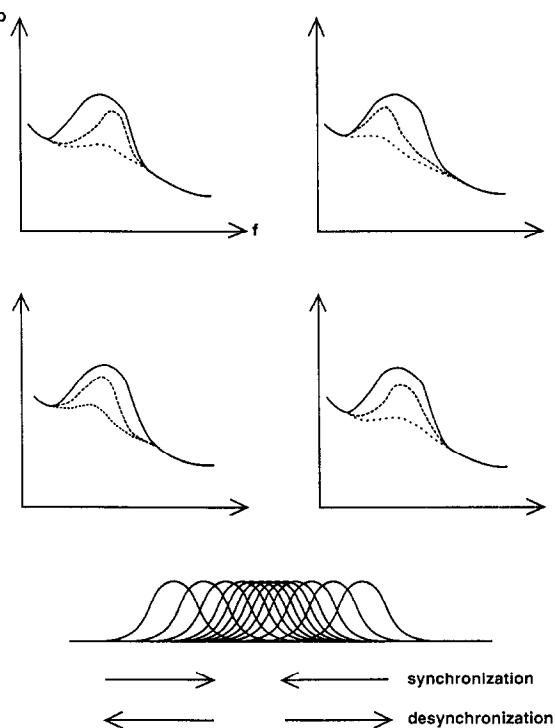


Fig. 3. Task difficulty is one of the most powerful factors leading to a pronounced alpha desynchronization. Alpha desynchronization may be explained in terms of a large population of alpha oscillators responding to task demands by shifting their frequency.

average of 16 data points. Based on these computations, the percentage of an increase or decrease in band power is calculated for each electrode and experimental condition according to the following simple equation:  $ERD\% = ((band\ power\ reference\ interval - band\ power\ test\ interval) / (band\ power\ reference\ interval)) * 100$ . A positive ERD value indicates a decrease in band power whereas a negative value indicates an increase in band power with respect to the reference interval. Thus, positive values reflect a state of desynchronization, negative values a state of synchronization or ERS (event-related synchronization, cf. Pfurtscheller, 1992).

When applying this method, the most basic finding is that those cortical areas which are involved in the processing of a task tend to desynchronize, whereas other areas which most likely are not primarily involved either tend to synchronize or show no power changes at all. Examples of ERD maps showing the encoding of a visually presented word and the preparation for a verbal response (c.f., Pfurtscheller and Klimesch, 1992a, Pfurtscheller and Klimesch, 1992b) are shown in Fig. 4. These examples are taken from an experiment in which subjects

had to perform a simple semantic judgment task. They were asked to respond verbally with 'yes' if a word belongs to the superordinate concept 'animal' and to respond with 'no' if it belongs to 'tools'. As the results indicate, parieto-occipital areas are desynchronized during the semantic encoding of a word, whereas central and frontal regions show an increase in alpha power and, thus, are synchronized. During the verbal response, however, the picture reverses. Now parieto-occipital areas appear synchronized, whereas central areas (over the homunculus) are desynchronized. Note that the depicted ERD results were found within the frequency range of the upper alpha band.

The most general conclusion from this and a variety of other studies, is that activated areas desynchronize, whereas not specifically activated regions synchronize. Further findings have revealed that complex and difficult tasks show (i) a significant higher level of desynchronization with (ii) a longer lasting duration of desynchronization and (iii) a more widespread topographical distribution of desynchronization than less complex and easy tasks. These basic results were obtained not only for motor tasks

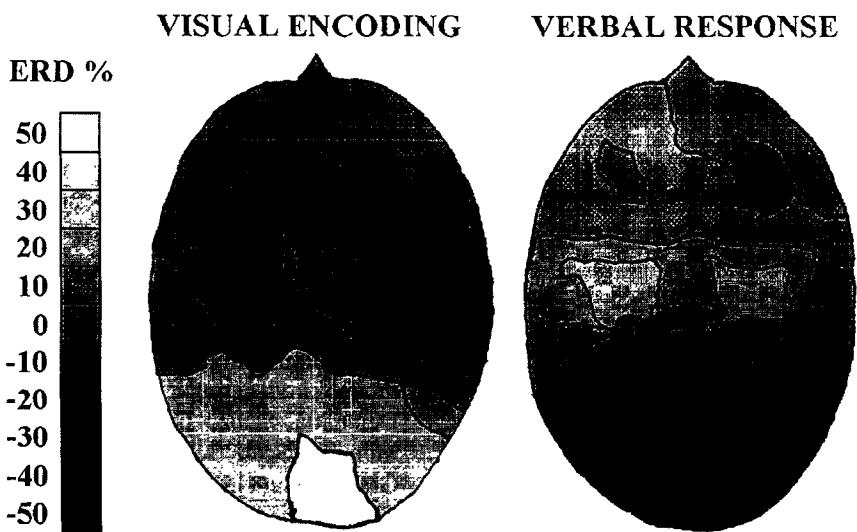


Fig. 4. Event-related band power changes as measured by 'event-related desynchronization' (ERD) reflect the percentage of an increase or decrease in band power during a test interval with respect to a reference interval (for details see e.g., Pfurtscheller and Klimesch, 1992a; Pfurtscheller and Klimesch, 1992b). Positive ERD values reflect a process of desynchronization (decrease in band power), negative ERD values a process of synchronization (increase in band power). The example shows that alpha desynchronization is a topographically restricted phenomenon that can be observed over those brain areas that are involved in performing a particular task. During the encoding of visual information, parieto-occipital areas are desynchronized, whereas during a verbal response central regions are desynchronized.

with varying complexity or difficulty (e.g., Pfurtscheller and Berghold, 1989) but also for cognitive tasks (Boiten et al., 1992; Klimesch et al., 1990a; Klimesch et al., 1990b; Klimesch et al., 1992; Klimesch et al., 1993a; Klimesch et al., 1993b; Klimesch et al., 1994; Klimesch et al., 1996a; Klimesch et al., 1996b; Klimesch et al., 1996c; Sergeant et al., 1987).

### 2.3. Alpha frequency and memory performance

Before actually testing the proposed hypothesis that alpha frequency varies as a function of memory performance, it is important first to show to what extent (i) alpha frequency varies interindividually and (ii) what in general the factors are that affect interindividual differences in alpha frequency. If alpha frequency would not show a significant interindividual variability the proposed hypothesis could be rejected before considering more complex experimental designs. However, as a variety of studies have shown, alpha frequency varies to a considerable extent even in normal and age matched subjects, showing a quite constant standard deviation of 1 Hz (Köpruner et al., 1984; Klimesch et al., 1990a; Klimesch et al., 1993a, Klimesch et al., 1993b). Based on the fact that young normal adults at an age of about 30 years show a mean alpha frequency of about 10 Hz and a standard deviation of 1 Hz, a normal distribution as depicted in Fig. 5 gives quite reasonable results. According to the normal distribution, 95% of all subjects will have an alpha frequency lying within a range of 8 to 12 Hz. Interindividual differences are quite large. As an example, we see that 32% of the subjects are expected to show a difference in alpha frequency that exceeds 2 Hz.

With respect to the factors that influence alpha frequency, it is well known that alpha frequency decreases with increasing age. Köpruner et al. (1984) have found a linear relationship ( $\text{alpha peak frequency} = 11.95 - 0.053 * \text{age}$ ) within the age range of adult subjects. As an example, according to this relationship, a young adult of, e.g., 20 years has an expected peak frequency of 10.89 Hz, whereas a 70-year-old subject shows a drop of 2.65 Hz down to a frequency of 8.24 Hz. However, as we already have mentioned, even in a sample of age matched subjects, alpha frequency shows a large interindividual variability that can be described in terms of a

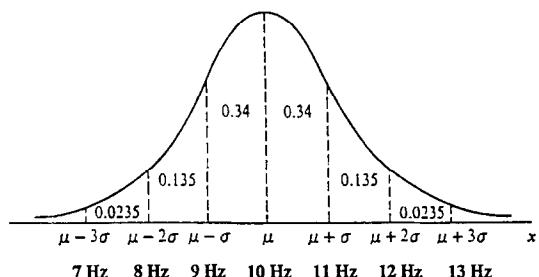


Fig. 5. Interindividual differences in alpha frequency are large, even within a group of age matched subjects. They can be described by assuming a normal distribution. Experimental data indicate that alpha frequency for young adults of about 30 years of age show a mean of 10 Hz and a standard deviation of 1 Hz (e.g., Köpruner et al., 1984 and Klimesch et al., 1990a). When assuming a normal distribution with  $\mu = 10$  Hz and  $\sigma = 1$  Hz, 95% of all subjects are expected to have an alpha frequency that lies within a range of 8 to 12 Hz. This is a quite realistic estimate that also is close to the figures of the standard normal distribution.

normal distribution (c.f., Fig. 5). Clinical evidence demonstrates that a variety of brain diseases lower alpha frequency. At the first glance this latter fact does not seem relevant with respect to our hypothesis because it may be objected that a decreased alpha frequency is only one aspect of a generally slower EEG in neurological patients. There are, however, reports that even in neurologically impaired patients a decrease in alpha activity might be selectively related to a decrease in memory performance. Sheridan et al., 1988 compared two groups of Alzheimer patients, one Group (Group A) showing regular alpha waves during eye closure (in the frequency range of 9–13 Hz) and attenuated by eye opening and a second Group (Group B) showing only irregular mixed frequency slow alpha (in the range of 7–11 Hz) without attenuation by eye opening. Most interestingly, Sheridan et al. (1988) report that although both groups did not differ on the Mattis Dementia Scale, Group A had higher Wechsler Memory Scale scores (87 as compared to 70 in Group B) and higher parietal glucose metabolic rates. The reported differences were only marginally significant.

These preliminary results are quite consistent with the proposed hypothesis of a relationship between alpha frequency and memory performance. The fact that alpha frequency shows a strong variability provides the basis for relating interindividual differences

in alpha frequency to interindividual differences in memory performance. Furthermore, the fact that alpha frequency declines with age and a variety of neurological diseases also is plausible on the basis of the suggested hypothesis. With increasing age, memory performance tends to decline too as it does as a result of a variety of brain diseases. Although supporting our hypothesis, the reported results are still quite general and unspecific. In order to provide a critical test for the proposed hypothesis, alpha frequency must be measured also during actual memory performance under experimental conditions.

The requirement to measure alpha frequency during actual memory performance has an important methodological consequence. As we already know, alpha desynchronizes during mental activity and as a result, the power distribution becomes quite flat. Thus, peak frequency as the traditional measure for alpha frequency no longer is an appropriate measure because in a flat distribution which quite often shows multiple flat peaks, it is arbitrary to select just the highest power value (i.e. the 'peak'). In such situations, the calculation of gravity frequency is a reasonable choice for measuring alpha frequency. A more general reason to use gravity instead of peak frequency refers to the fact that gravity frequency reflects a property of the entire shape of the power distribution and, therefore, is a more adequate measure to reflect a property of the entire population of alpha frequencies.

Unlike peak frequency, gravity frequency can be only defined within a specified frequency window and as a consequence varies with the selected frequency range. Using a fixed range (e.g., 8–13 Hz) when calculating gravity frequency does not make much sense. Due to interindividual differences in alpha frequency, for some subjects parts of the alpha power distribution will fall outside a fixed range. As a consequence, gravity frequency would be distorted and would not reflect interindividual differences in an adequate way. A promising way to avoid this problem is first to define the frequency range of the alpha power distribution individually for each electrode and each subject and then to calculate gravity frequency within that frequency window (see Klimesch et al., 1990a for a description of the respective method). This method results in an extended alpha band on the average, and, thus, to avoid confu-

sion with conventional measures we use the term Individual Alpha Frequency (IAF).

IAF was used as indicator of alpha frequency in a series of experiments. In Experiment 1 of Klimesch et al. (1990a), IAF was measured during a resting period in a sample of demented Alzheimer subjects (mean age = 71.5; SD = 7.76) who were also tested with the Wechsler Memory Scale. Based on their overall quotients, subjects were divided in two groups, in a group with (comparatively) good memory (denoted M+ with a mean age of 72 years) and in a group with bad memory (denoted M- with a mean age of 70 years). Comparing mean IAF between the two groups (M+: 8.14 Hz; M-: 7.02 Hz) shows that alpha frequency differs in the predicted direction. Alzheimer subjects with good memory show an alpha frequency which is 1.12 Hz higher than Alzheimer subjects with bad memory. It is important to note that despite the differences in alpha frequency, the overall EEG frequency did not differ with respect to memory performance. Correlations computed for individual IAF at all leads (the EEG was recorded from 19 electrodes) and the overall Wechsler scores over the entire sample revealed that at all recording sites of both hemispheres alpha frequency correlates significantly with memory performance as measured by the Wechsler Memory Scale. Thus, in agreement with the findings of Sheridan et al. (1988) our study provides additional support for a selective relationship between alpha frequency and memory performance. A weak, but not significant relationship between verbal memory and alpha frequency was reported by Saletu and Grünberger (1985). However, in contrast with our study and with that of Sheridan et al. (1988), Saletu and Grünberger (1985) used fixed frequency bands. From control computations with our own data we know that fixed frequency bands tend to blur a significant relationship between IAF and memory performance. This is not surprising, because, as we have already emphasized, due to interindividual differences significant portions of the alpha power distribution fall outside a fixed frequency band, thus biasing the measurement of alpha frequency. The use of fixed frequency bands might very well have prevented other researches from detecting a relationship between alpha frequency and memory performance (e.g., Surwillo, 1971)

The data reported so far refer to alpha resting frequency. The interesting question, thus, is whether alpha frequency shifts from a reference interval to a test interval in which subjects actually are retrieving information from memory. In Experiment 2 of Klimesch et al. (1990a) subjects performed a verbal recognition test and IAF was measured during a test interval of 1 s in which a subject was correctly recognizing a word and in a reference interval (of also 1 s) which preceded the test interval by 2 s. The results confirmed the findings of Experiment 1 and demonstrate again that, as compared to bad memory performers, good performers have an IAF which is more than 1 Hz higher. However, when comparing the reference with the test interval, neither an in-

crease in IAF nor an increase in the significance of correlation coefficients between IAF and memory performance could be found. Fig. 6 gives an overview of the respective results.

An important argument that may threaten the validity of our hypothesis refers to the fact that the results, reported so far, could theoretically also be explained in terms of interindividual differences in attention. It could be objected that the higher IAF of good memory performers reflects a state of increased attention which is responsible for an increase in memory performance. There is ample evidence that alpha desynchronization may reflect attention (e.g., the classical work of Mulholland, 1969). This objection may appear particularly plausible within the

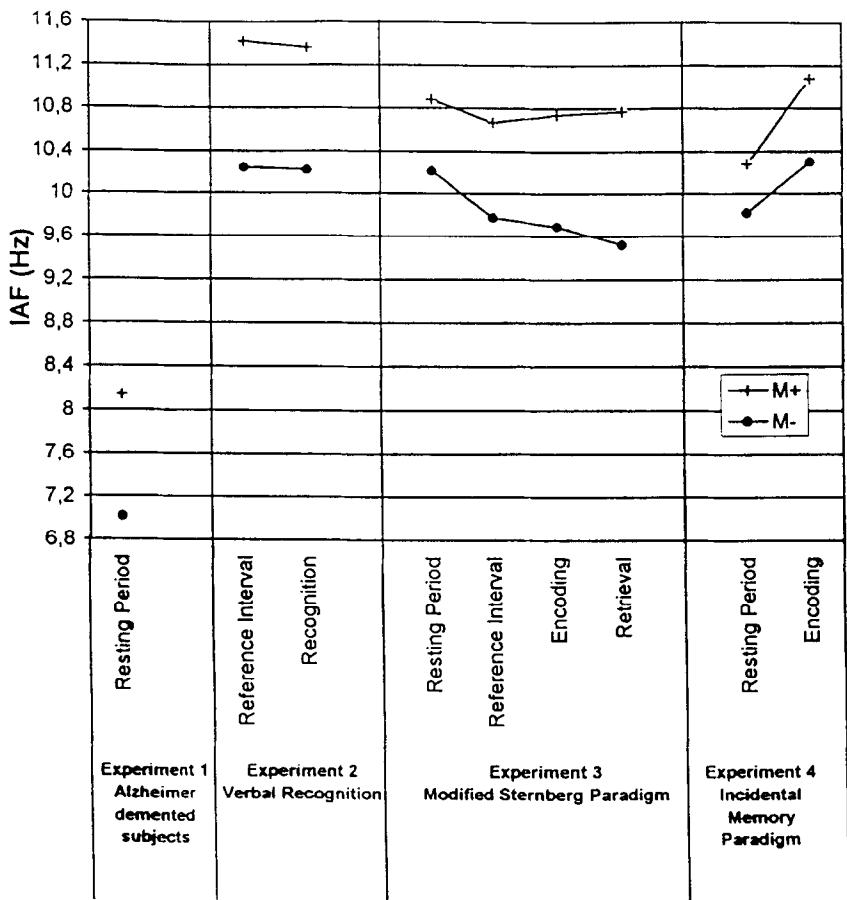


Fig. 6. As compared to bad memory performers, good performers have a significantly higher alpha frequency even during a resting period. The experimental manipulation of attentional demands has no significant negative effect on this relationship. The reported results were found in four independent experiments (Klimesch et al., 1990a; Klimesch et al., 1993a; Klimesch et al., 1996a).

context of Experiment 2, because IAF was measured during actual memory performance that of course also requires attentional resources. It is, however, less likely that resting IAF as measured in Experiment 1 also reflects attentional resources. For the resting period, subjects were asked to relax and, thus, interindividual differences in attention are an unlikely factor to determine differences in IAF. In support with this interpretation, Treisman (1984) has shown that intraindividual fluctuations in alpha frequency obviously are too small to account for fluctuations in attention. We assume that even during a resting state, the potential processing capacity of the thalamo-cortical network might very well be reflected by IAF.

In order to test the possible objection that IAF may reflect attentional instead of memory processes, a specially designed experiment (denoted Experiment 3 in the following) was carried out by Klimesch et al. (1993b). In this study, a modified version of Schneider's and Shiffrin's memory search paradigm (c.f. Schneider and Shiffrin, 1977) was used which allows to vary attentional and memory demands in an orthogonal design. In each trial subjects viewed a string of 5 or 10 characters (termed 'memory set') which they are asked to retain in memory. Then, after an interstimulus interval of 2 s, a single character (letter or number) appeared (termed 'frame'). If the frame is an element of the memory set, it is called a target, otherwise a distractor. Subjects were asked to respond with 'yes' to a target and with 'no' to a distractor. Attentional demands are varied by using either the same memory set across a series of trials (termed consistent mapping condition) or different memory sets with different characters (termed varied mapping condition). Under the consistent mapping condition, subjects knew which characters the memory set on the next trial will contain. Under the varied mapping condition, each memory set contains new characters. Thus, when deciding whether a frame is a target or distractor, subjects must be careful not to confuse characters between the current and the previously shown memory set. According to Shiffrin and Schneider, selective (or focused) attention refers to those control mechanisms which allow a subject to encode a sensory input into memory. The concept of selective attention is closely linked to that of limited capacity. If processing capacity is

overloaded, attention becomes divided and performance is reduced. As an example, if the memory set comprises only a single character, attention is 'focused' on the target. But with increasing memory set size, attention also becomes increasingly 'divided' and processing capacity overloaded. This design allows us to vary attentional demands (as manipulated by the two mapping conditions) and memory demands (as manipulated by memory set size) as independent factors while using selected groups of good and bad memory performers as subjects.

If attention were the only relevant factor, IAF should vary as a function of attentional demands. If, on the other hand, memory performance is the only relevant factor, IAF should vary as a function of memory demands. Increased attention will result in increased memory performance. Because memory performance is reflected by IAF, we have to assume that both, attentional and memory demands vary with IAF. The crucial prediction, however, is that the manipulation of attentional demands does not blur or abolish the frequency difference between good ( $M +$ ) and bad memory performers ( $M -$ ). As the pronounced differences between good and bad memory performers show (cf. the right part of Fig. 6), this prediction is supported by the results of Experiment 3.

It is important to note that the variation of attentional demands has affected IAF only in the range of a tenth of 1 Hz. Consistent effects in the sense that increasing attentional load leads to a decrease in IAF were found at central and parietal leads only.

Differences in memory demands (encoding of  $n = 5$  or  $n = 10$  items; denoted  $n5$  and  $n10$ , respectively) are somewhat more pronounced but still lie within the range of a tenth of 1 Hz. In contrast to attentional demands, the effects of memory demands are very consistent for different recording sites in both groups of subjects. While keeping in mind that good and bad memory performers differ in the range of about 1 Hz, the experimentally induced differences lying in the range of only a tenth of 1 Hz are extremely small.

With respect to task difficulty, the general pattern of results is that event-related shifts in alpha frequency show a tendency to decrease with increasing task demands. The strongest effect by far is a highly significant drop in IAF for bad memory performers

of about 0.7 Hz with increasing experimental demands (cf. the drop in IAF for bad memory performers from the resting to the retrieval period in Fig. 6). This fact is particularly interesting because it demonstrates that the magnitude of event-related shifts in IAF may be much larger than the differences in IAF which were observed in response to variations in attentional and memory demands as mentioned above. This tonic shift in IAF for bad performers, which most likely reflects a general effect of increasing task difficulty does not blur, but instead increases the group differences between good and bad performers.

The use of an individually adjusted alpha band was essential for observing the relationships described between task demands and alpha frequency, as control computations on our own data have revealed. Results reported in the literature are based on fixed frequency bands. Thus, it does not come as a surprise that in response to increasing task demands in some experiments an increase as well as a decrease in alpha frequency was found (e.g., Earle, 1988) whereas in other experiments only a decrease was reported (Zeller and Bente, 1983). We have already emphasized that because of large interindividual differences, significant portions of the alpha power distribution will fall outside a fixed frequency window. As an example, let us consider a subject with a low alpha frequency and let us assume that the lower alpha band falls below the frequency window of the fixed band which then covers only the upper alpha and some portions of lower beta. Consequently, a decrease or increase in frequency (i.e., a desynchronization or synchronization) of the lower alpha band cannot be detected in this case if a fixed band is used.

#### 2.4. Alpha desynchronization and memory performance

When interpreting shifts in alpha frequency, we have to keep in mind that mean gravity frequency or IAF reflects the behavior of an entire population of different alpha frequencies. According to this view, a shift in IAF is not due to a frequency shift of a single alpha rhythm. A shift in frequency simply means that the power of some alpha frequencies may increase whereas others decrease. As we have emphasized, a

power increase is interpreted in terms of synchronization (large cell populations respond with frequencies in a very narrow band) whereas a decrease in power is interpreted in terms of desynchronization (many but comparatively small cell populations respond with different frequencies). The question now is, how many frequencies there are and which frequencies of the entire population tend to change their power more than others. The first question is very difficult to answer, the second, is not. The results obtained from principal component analyses performed to define major spectral bands in the EEG have repeatedly shown that power values in the alpha band load on two different and orthogonal components (e.g., Mecklinger et al., 1992) with highest loadings in the lower and upper alpha band. As an example, Mecklinger et al., 1992; (p. 114, Fig. 6) found two orthogonal components in the alpha band, one with highest loadings between 7 and 11 Hz and a second with highest loadings between 10 and 13 Hz. The overlap between the two components, thus, occurs between 10 and 11 Hz which is exactly that range where the peak frequency in a resting period (not reported by Mecklinger et al.) is to be expected for a sample of young subjects (Mecklingers subjects had a mean age of about 21 years). Taken together, these data indicate that power values of the lower and upper alpha band vary largely independent from each other and that resting alpha frequency marks (or is even created by) the overlap between the two alpha bands. Thus, instead of a single population of alpha frequencies, we have to deal with two different populations that operate largely independently from each other.

Reinterpreting our data on the basis of this evidence supports the idea that a decrease in IAF is due to a tendency towards desynchronization which is more pronounced in the upper than in the lower alpha band. Any attempt towards a more precise interpretation, thus, depends on an understanding of the functional difference between the lower and upper alpha band.

According to these interpretations it is questionable whether DURING desynchronization, frequency shifts are 'real' in the sense that they reflect the speed of information processing. The selective desynchronization in different frequency bands within the alpha frequency range might very well blur real

shifts in frequency. Although interesting in itself, the question whether or not frequency shifts during desynchronization are real is not relevant for testing our hypothesis.

#### *2.4.1. The lower alpha band reflects attentional processes*

In terms of alpha power desynchronization, a decrease in alpha frequency indicates that the upper alpha band shows a more pronounced desynchronization than the lower alpha band. Therefore, it is to be expected that bad performers with their pronounced drop in alpha frequency show a large desynchronization in the upper but a weak desynchronization in the lower alpha band. When analyzing the data of Experiment 3 on the basis of event-related power changes in the individually determined lower and upper alpha band, this expected result can indeed be observed. Whereas good and bad memory performers show a large desynchronization in the upper alpha band which is somewhat more pronounced for bad performers, bad performers lack any significant desynchronization in the lower alpha band during retrieval. A similar but somewhat weaker tendency was also found for the encoding interval. The conclusion, therefore, is that bad memory performance is related to a weak or insufficient desynchronization of the lower alpha band. But what is the meaning of this result?

When trying to interpret the differences in the lower alpha band for good and bad memory performers, it is necessary to focus on the functional meaning of the two alpha bands. Inspecting the time course of ERD in several experiments has revealed that the effect of the response signal is a strong short-lasting synchronization which appears in the lower alpha band only (e.g., Klimesch et al., 1993b). Subjects were instructed to wait with their response until the response signal appeared two seconds after a target or distractor was presented. The short-lasting synchronization in the lower alpha band indicates the occurrence of an expected event on which the subject gives an overt response to a decision he or she already knows. Thus, the effect of the response signal in this experiment obviously is to induce a shortlasting relaxation which is correlated with a decrease in attention.

Some clarifying remarks will be useful with re-

spect to the meaning of the concept ‘attention’. Psychological theories of attention usually focus on two different questions (cf. Treisman, 1986). One refers to those mechanisms underlying the allocation of limited processing resources, the other to selective attention. These two aspects are also stressed by Posner (e.g., Posner and Boies, 1971) who distinguishes between three components of attention: alertness, selectivity, and processing capacity (for an extensive review see Posner, 1975). Alertness — a concept closely related to arousal, which Posner avoids because of its emotional connotation — is further subdivided into phasic and tonic alertness. Phasic changes in alertness are under volitional control and occur at a rapid rate, whereas tonic changes are not (or less) under volitional control and occur at a much slower rate. A typical example of a phasic change is the increase in alertness after the presentation of a warning signal. Tonic changes, on the other hand, occur as a function of fatigue, distress, circadian rhythms and changes over the life cycle. According to Posner, alerting stimuli such as a warning signal have no selective effects on information processing. Selective effects are due to ‘pathway activation’ which serves to activate particular memory traces. According to this view, selective attention and phasic alertness are essential requirements for any cognitive process. A memory search as an example of a cognitive process will be guided by selective attention, whereas phasic alertness is a comparatively distributed mechanism which allocates — or prepares to allocate — processing resources.

In Klimesch et al. (1992), the effects of phasic alertness on the two alpha bands were studied. In one of the two experiments, subjects were required simply to read a series of words and numbers. The only experimental manipulation was the variation of the time period between the presentation of the warning signal and the presentation of a word or a number. According to this manipulation, the warning signals (denoted W1, W2, W3) appeared randomly either 1, 2 or 3 s before the imperative stimulus. The results are depicted in Fig. 7 and demonstrate that the effect of the warning signal shows up in the lower alpha band only. These findings were replicated in yet another experiment in which the additional effects of expectancy were investigated (Klimesch et al., 1992, Experiment 2).

In contrast to the response signal in Klimesch et al. (1993a) which reminded the subject to respond, an alerting effect can be observed in Fig. 7. The alerting effect is denoted by a phasic desynchronization of the lower alpha following the presentation of a randomly spaced warning signal (W1, W2 and W3). Comparing the time course of desynchronization in the two alpha bands reveals that the largest change in alpha power was found for the lower alpha band in response to the imperative stimulus. This result, which was replicated in Experiment 2 of Klimesch et al. (1992) indicates that although a warning signal makes a subject more alert, the strongest increase in alertness — most likely reflecting the allocation of processing resources — is associated with the encoding of the imperative stimulus. In the upper alpha band, the time course of desynchronization shows a strikingly different pattern. Here, desynchronization occurs in response to the encoding of the imperative stimulus, whereas the effects of the warning signals are completely lacking. Because of the divergent results found for the two alpha bands, it seems plausible to assume that the upper alpha band responds selectively to the encoding of the stimulus, whereas the lower band reflects attentional processes. This interpretation is in good agreement with the fact that, compared to the lower band, the increase in ERD is much more localized in the upper band with maximal desynchronization at parietal and occipital recording sites (cf. Fig. 7). Because of the visual-verbal nature of the task in both experiments of Klimesch et al. (1992), these brain areas would have been expected to exhibit the most significant desynchronization, i.e., increase in ERD.

The suggested hypothesis concerning the functional difference of the two alpha bands was also tested in an experiment which analyzed the 'Dm effect' (see below) by means of ERD in an incidental memory paradigm in which subjects had to perform a semantic judgement task with those words which were later tested in a free recall task (Klimesch et al., 1996a). The Dm effect (or simply 'Dm' for differences based on later memory performance; Paller et al., 1987) refers to the result that during the encoding of pictures or words that were remembered in a later recall or recognition test, some components of the event-related brain potential (ERP) are significantly

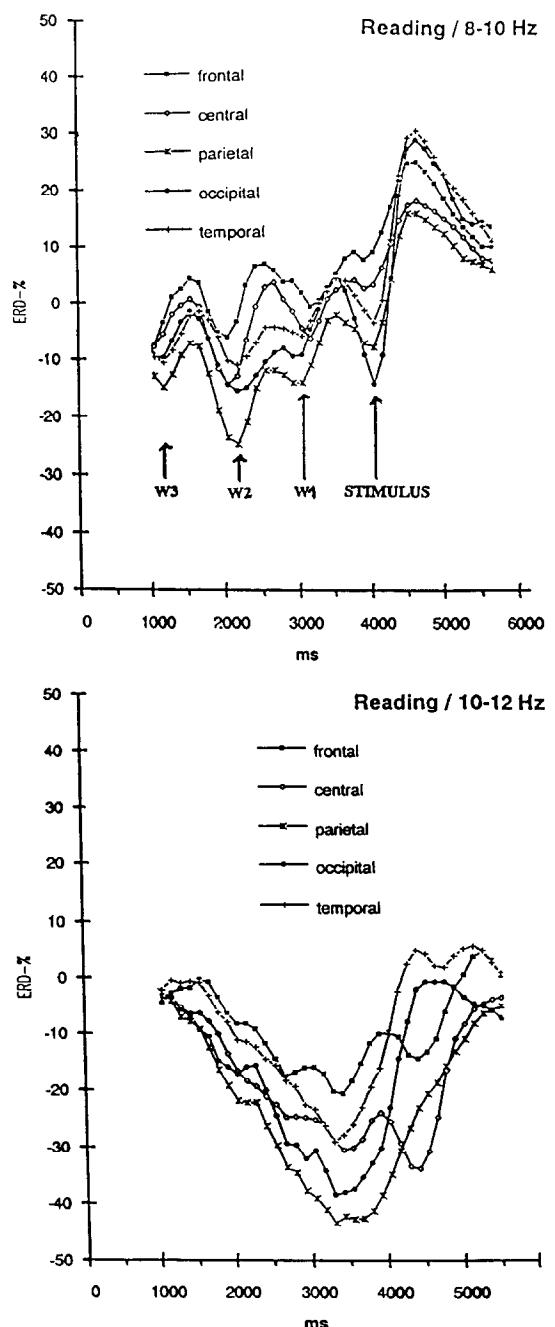


Fig. 7. Event-related band power changes, measured by ERD. Only the lower alpha band reflects the alerting effect of a warning stimulus. The upper alpha band, on the other hand, only responds to the encoding of the imperative stimulus, which in this case is a word. The subjects task simply was to read a word.

more positive going than for items which cannot be remembered.

A specific prediction regarding a Dm effect in the alpha band can be made when considering the different functional meaning of the lower and upper alpha band together with the results of the above reported study of Klimesch et al. (1993a). In this study, we have found that good memory performers (as compared to bad memory performers) show a somewhat weaker desynchronization in the upper alpha band, but a significantly stronger desynchronization in the lower alpha (for related results see also Klimesch et al., 1990a). We have proposed that this result indicates that good memory performers need less effort to encode a stimulus (therefore, they show only a weak desynchronization in the upper band) but that they increase their level of alertness during the encoding of a stimulus (therefore, they show a stronger desynchronization in the lower alpha band).

On the basis of this interpretation, the following type of Dm effect can be expected. For good performers we would expect a positive Dm effect (larger desynchronization for those items which are remembered in a later free recall task) in the lower alpha band, reflecting increased alertness for those words which can be remembered later. Bad performers, on the other hand, put more effort in the semantic encoding and/or processing of the stimulus. Thus, those words, they remember should show a positive Dm effect in the upper alpha band. The strongest Dm effect which appeared over parietal recording sites supports this prediction and shows that good performers show a positive Dm effect in the lower alpha band, whereas bad performers show a positive Dm effect in the upper band.

These findings show that the lack of desynchronization (or synchronization) in the lower alpha band is related to a lack of alertness or attention in general. In supporting this interpretation Crawford et al. (1995) have found that in contrast to subjects with high sustained attention, low sustained attention subjects who have difficulty inhibiting distracting environmental stimuli show a significantly larger proportion of lower alpha power.

#### *2.4.2. The upper alpha band reflects semantic memory processes*

In a recently performed experiment, we (Klimesch et al., 1994) have tested the hypothesis that semantic

long term memory (LTM) processes are primarily reflected in the alpha band (or higher frequencies such as beta or gamma which are not considered here), whereas episodic encoding processes in working memory are reflected in a different frequency band, possibly in the theta band (for a more detailed discussion of this issue see also Klimesch et al., 1994; Klimesch et al., 1996b, Klimesch et al., 1996c). In the experiments reported so far (as well as in most experiments reported in the literature), semantic and episodic memory processes play an important role. Because of a close interrelation between episodic and semantic processes which we will consider in section 5 below, a critical test of whether or not the alpha band selectively responds to semantic memory demands requires a carefully planned experimental design. In the study of Klimesch et al. (1994) we relied on a design that already proved useful to distinguish semantic from episodic retrieval processes (see Experiment 4 in Kroll and Klimesch, 1992). In this study of Kroll and Klimesch (1992) in which the memory speed effect was tested, we have found that complex concepts speed up semantic decision, but slowed down episodic recognition times. The experimental design consisted of two parts. Subjects first performed a semantic congruity task in which they had to judge whether or not the sequentially presented words of concept-feature pairs (such as 'eagle-claws' or 'pea-huge') are semantically congruent. Then, without prior warning, they were asked to perform an episodic recognition task. This was done in an attempt to prevent subjects from using semantic encoding strategies and thus to increase episodic memory demands. In the episodic task, the same concept-feature pairs were presented together with new distractors (generated by re-pairing known concept-feature pairs). Now subjects had to judge whether or not a particular concept-feature pair was already presented during the semantic task. The most important features of the design are shown in Table 1.

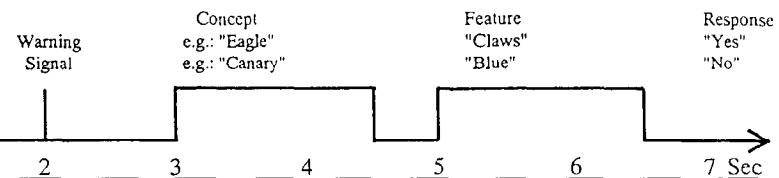
The experimental design shows three important features. First, in both tasks, the semantic and episodic task a response can be made only after the second item of a pair (i.e., the feature) is presented. Second, only correct yes responses were analyzed. This means that with the exception of task type, all other factors such as response type and stimulus words were kept constant. Third, from the results

Table 1

Structures of single trials and experimental designs

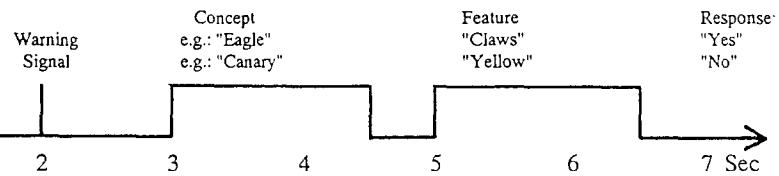
## Semantic task

Subjects judge whether the feature is semantically congruent with the concept. Half of all pairs is congruent, the other half incongruent.



## Episodic task

The congruent pairs of the semantic task are now the targets. Distractors consists of the concepts of incongruent pairs, but were re-paired with features from other known pairs in such a way that they are now also congruent. Subjects judge whether or not a pair was already presented during the semantic task.



found in Kroll and Klimesch (1992) we know that the episodic task (showing longer RT's and a larger percentage of incorrect responses) is much more difficult than the semantic task. This latter feature of the design is important for our central prediction which is that the upper alpha band desynchronizes selectively in response to semantic task demands. However, while keeping in mind that alpha desynchronizes with increasing task difficulty, one would expect the opposite effect, which is a stronger desynchronization during the episodic task. Thus, if task difficulty were the only factor which was reflected by an event-related decrease in the upper alpha band (i.e., an increase in ERD) we would expect the most pronounced increase in ERD to be observed during the presentation of the feature in the episodic task. This, however, is not the case. The results indicate that in spite of the fact that the semantic task is easier than the episodic task, the upper alpha band shows a significantly stronger desynchronization during the processing of the feature in the semantic task (cf. Fig. 9).

The different time course of desynchronization for the concept and the feature in the semantic task is

depicted in Fig. 8. We see that the strongest desynchronization occurs at about 500 ms post-stimulus during the processing of the feature word. In the episodic task the time course of desynchronization is strikingly different. As we know from RT-studies focusing on the decomposition of different processing components, the semantic encoding and processing of an isolated word takes place at about a time interval of 400 to 600 ms post-stimulus (Klimesch et al., 1987). Taken together, the results provide strong evidence for the view that the upper alpha band is related to the processing of semantic LTM information.

Fig. 9 gives a summary of the results with respect to the three frequency bands that were analyzed in this experiment. The following findings are of primary importance: (i) During the processing of the feature word, the upper alpha and the theta band show the expected selective effects with respect to task type. Whereas the upper alpha desynchronizes in response to semantic task demands, theta synchronizes during episodic demands. (ii) The lower alpha — presumably reflecting attentional demands — responds to task difficulty. During the processing of

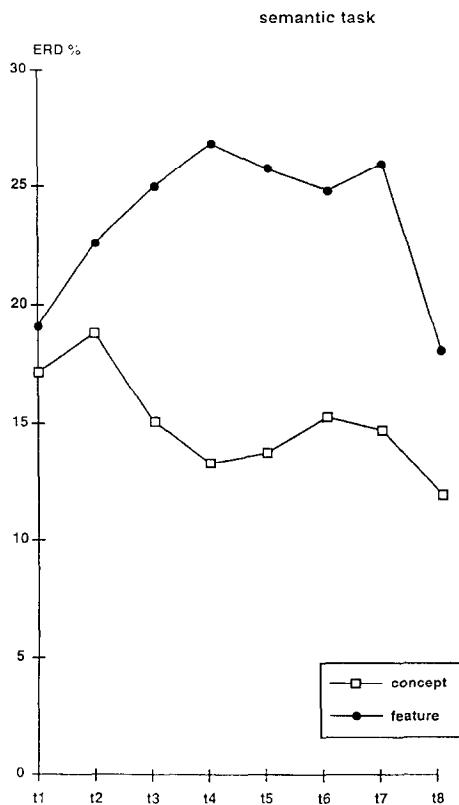


Fig. 8. Event-related band power changes, measured by ERD. The upper alpha band responds selectively to semantic memory demands. In a semantic congruity task, in which concept-feature pairs were to be judged (the experimental design is depicted in Table 1), the amount of upper alpha desynchronization reaches a maximum during that time interval in which the semantic congruity or incongruity can be judged. This is about 500 ms after the feature word is presented.

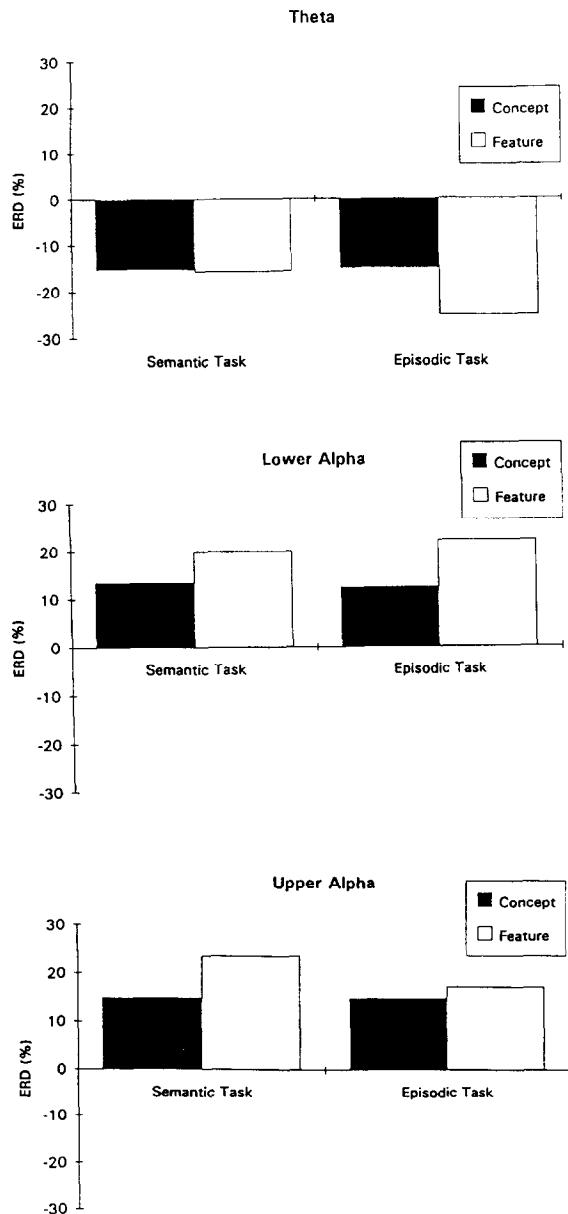
the feature word and during the episodic task in particular the lower alpha band is desynchronizing. (iii) Finally and most importantly, the theta band

Fig. 9. Event-related band power changes, measured by ERD. Comparing event-related power changes in the theta and the two alpha bands reveals that with increasing task demands theta synchronizes whereas alpha (in both bands) desynchronizes. Theta synchronization is selective with respect to episodic memory demands, whereas upper alpha desynchronization is selective with respect to semantic memory demands. Note that despite the fact that the episodic task is much more difficult, upper alpha desynchronization is more pronounced in the semantic task. In contrast to the upper alpha band, the lower alpha band seems to reflect attentional demands which are more pronounced during the processing of the feature and in the episodic task.

synchronizes with respect to task demands, whereas the opposite holds true for the alpha band. The important implication of this latter fact is to assume that different neuronal generators are involved in producing theta and alpha frequencies.

## 2.5. Interim conclusions

The experimental results reported in this section show that the frequency of the alpha rhythm is



related to memory performance. As a consequence of this finding it can be assumed that the memory speed effect is related to the frequency (or ‘speed’) of the alpha rhythm.

Alpha frequency is a measure reflecting the activity of both, the upper and the lower alpha band. Because it was found that (i) the upper alpha band is related to semantic LTM demands and that (ii) attentional demands do not blur the relationship between alpha frequency and memory performance, it can be concluded that alpha frequency reflects the speed of cognitive processes in semantic LTM.

All of the reported results were found within narrow frequency bands that were individually adjusted for each subject by using the individual alpha (peak or gravity) frequency as an anchor point. Control computations which were based on the traditional fixed frequency bands in the alpha range blur the reported effects to the extent that they are no longer statistically significant.

In a more general sense, our data document that (i) EEG frequencies vary interindividually to a great extent (ii) EEG frequencies are very subtle indicators of cognitive processes provided that frequency bands are determined individually, and (iii) different types of cognitive processes are reflected by different EEG frequencies within a narrow frequency window. The most general conclusion is that memory processes can be described in terms of brain rhythms or brain oscillations. This idea forms the basis for the model outlined later in the paper.

Because there is evidence that EEG-alpha activity is related to thalamo-cortical oscillations (e.g., Steriade et al., 1990; Andersen and Andersson, 1968), it seems plausible to postulate a specific role of the thalamo-cortical network for memory processes. In trying to integrate our findings within a psychophysiological perspective, we suggest the following preliminary hypothesis which rests on three assumptions: (1) Memory codes are stored in the form of interconnected but widely distributed networks (cell assemblies) in the cortex. (2) Memory codes are accessed and retrieved via ‘longitudinal’ pathways linking deeper brain structures such as the thalamus and the hippocampal formation with the cortex. (3) Alpha is the dominant rhythm reflecting LTM processes.

### 3. EEG theta and memory

The findings of Klimesch et al. (1994) support the hypothesis that EEG theta activity is related to the retrieval of episodic information as the selective increase in theta synchronization during the processing of the feature word in the episodic task demonstrates (cf. Fig. 9). However, if EEG theta is related to episodic memory (or working memory) processes in general, it should be possible to demonstrate that not only the retrieval but the encoding process as well is reflected by a task-related increase in theta power. This prediction was tested in two recent studies (Klimesch et al., 1996b, Klimesch et al., 1996c). The results of Klimesch et al. (1996c) show that during encoding only those words that were later correctly recognized exhibited a significant increase in theta power. During the actual recognition processes, too, a significant theta synchronization was found for correctly remembered words only but not for distractions, as Fig. 10 demonstrates. Similar findings were obtained in an incidental memory paradigm (Klimesch et al., 1996b).

These and other findings (e.g., Arnolds et al., 1980) imply that the hippocampal theta rhythm may reflect the encoding and retrieval of episodic (or new) information in working memory. The crucial question, however, is whether it is reasonable to assume that the hippocampal theta rhythm may be induced into the cortex via hippocampo-cortical feed-back loops and, thus, may even be detected by scalp electrodes in the human EEG.

#### 3.1. Is (scalp) EEG theta related to hippocampal theta?

Since Scoville and Milner (1957) reported a severe anterograde amnesia for patient H.M., who had undergone a bilateral temporal lobectomy including the hippocampal formation, and since Green and Arduini (1954) found a dominant rhythmic electrical activity within the theta band in the hippocampus of rats, it became obvious that hippocampal theta might be related to the encoding and/or retrieval of new information. Positive evidence came from studies which have documented that there is a preference for long-term potentiation (LTP) to occur in the hip-

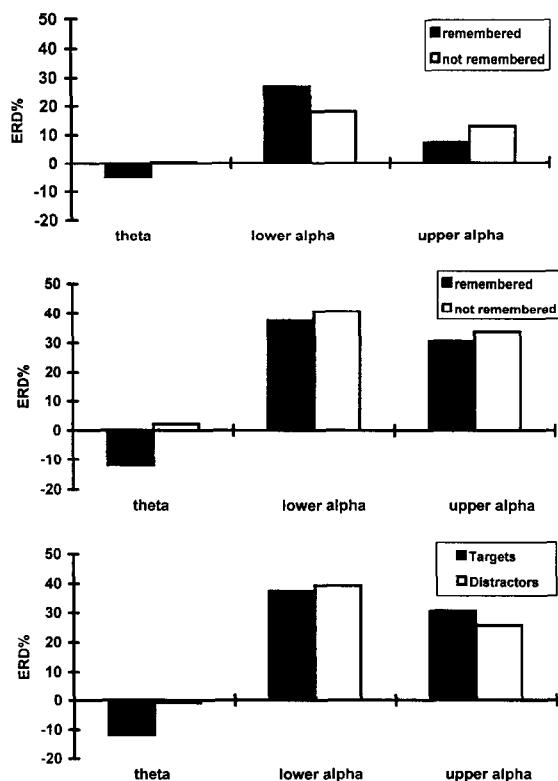


Fig. 10. Event related desynchronization (ERD), reflecting task related power changes for remembered and not remembered words in the theta, lower and upper alpha band. Subjects performed a recognition task. The EEG was recorded during encoding (in a study phase) and actual recognition (in a recognition phase). The results of the study phase (upper figure) and the recognition task (middle and lower figures) are plotted separately (cf. Klimesch et al., 1996c). Only words which were successfully encoded or retrieved exhibit a significant increase in theta power, i.e., show significant negative ERD-values. Note that already during the encoding process of those words that can later be remembered a significant increase in theta synchronization can be observed. In contrast, during the encoding of words which cannot be remembered later, theta band power did not increase.

pocampal formation, and that theta activity induces or at least enhances LTP (e.g., Larson et al., 1986 and Greenstein et al., 1988). The fact that LTP is considered the most important electrophysiological correlate for encoding new information, underlines the potential importance of hippocampal theta for working memory processes.

Because volume conduction is unlikely, the only way to explain that hippocampal theta can be detected by scalp electrodes is to assume that theta is

induced into the cortex via hippocampo-neocortical feed-back loops. It is well known that the hippocampal formation shows extensive projections to the neocortex from where it receives back-projections (cf. Miller, 1991 for an extensive review of this issue). These cortico-hippocampal feedbackloops could induce theta frequency in the cortex and, as a result, cortical theta should be possible to detect even with scalp electrodes.

How can this assumption of a specific relationship between hippocampal theta and scalp EEG theta be tested? If it can be demonstrated that hippocampal theta shows similar properties as compared to the EEG theta (recorded by scalp electrodes), a strong argument favoring this assumption would be at hand. More precisely, a relationship between hippocampal and EEG theta could be demonstrated by showing that hippocampal theta synchronizes with increasing task demands, just as EEG theta does. On the other hand, when seen from the perspective of (scalp) EEG, we have to expect that theta synchronization in the hippocampus is a narrow frequency band phenomenon because it is so well established that alpha (as the frequency band lying immediately above theta) is desynchronizing. As the results reported in the following will demonstrate, hippocampal theta shows the same type of task-related change as the EEG theta.

### 3.2. Important properties of hippocampal theta

Several terms have been used to denote the dominant EEG activity within the theta range recorded from the hippocampus of lower mammals. The most outstanding feature of the hippocampal EEG is a rhythmic slow activity (RSA) that can be observed if animals make voluntary movements (e.g., Vanderwolf and Robinson, 1981; Vanderwolf, 1992). The rhythmicity of the hippocampal EEG which shows up as a sharp peak in the power spectrum is one of the defining features of theta. In slow wave sleep (SWS) but also in alert, immobile animals the hippocampal EEG shows irregular slow activity (ISA) which sometimes also is called large irregular activity (LIA). Since it became known that RSA is mediated by different types of transmitters, two types of RSA or theta (termed type 1 and type 2 theta) were distinguished (see e.g., the review in Bland, 1985; Bland, 1986).

Hippocampal theta usually is described in terms of local field potentials that are recorded from micro-electrodes implanted in the CA1 and dentate layers of the hippocampal formation. Fig. 11 gives an example of a simultaneous recording of local field potentials and multi-unit discharges (see Bland, 1985, p.127 or Sinclair et al., 1982). Field potentials are assumed to reflect the summed and synchronous activity of a larger number of cells. Single or multi-unit recordings actually show neural discharges of a single or a group of cells respectively. The unit recordings reported here are all multi-unit recordings.

Fig. 11 shows several important facts. We first refer to the relation between hippocampal EEG (local field potentials) and behavior and then to the relation between EEG and multi-unit activity.

A regular theta with a high degree of rhythmicity is found during voluntary movements such as walking, jumping, etc. This type of very regular high frequency theta is called type 1 theta, the accompanying behavior, type 1 theta behavior. Type 1 theta frequency (in rodents) ranges from about 6.5 to 12 Hz. A somewhat slower and slightly more irregular theta frequency can be observed if sensory stimuli

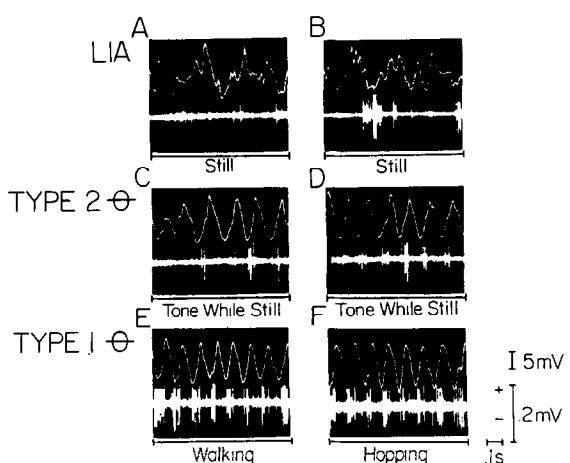


Fig. 11. Multi-unit discharges and local field potentials in the hippocampal dentate layer. (A) and (B) are examples of irregular discharge patterns during alert immobility. (C) and (D) reflect tone presentation during alert immobility. (E) and (F) show rhythmic discharges during walking and hopping. Note the increase in frequency from LIA to type 1 theta and the lack of unit discharge failures in type 1 theta. From Sinclair et al. (1982), reprinted with permission from the authors and the American Physiological Society.

are presented while animals are immobile but alert and, thus, in a state of arousal (Montoya et al., 1989). This type of hippocampal EEG is called 'type 2 theta' which varies within a range of about 4–9 Hz. Finally, a third type of behavior can be observed during 'automatic' motor patterns such as immobility, grooming, and chewing. Because during this automatic motor pattern, the EEG shows large irregular amplitudes, this type of behavior is also termed LIA behavior. Note that also during SWS a highly irregular slow EEG with even larger amplitudes can be observed. Thus, as compared to automatic motor patterns the LIA type EEG appears 'synchronized' during SWS.

When comparing the EEG (local field potentials) with multi-unit recordings, it can be observed that during high frequency type 1 theta the number of unit discharges is much higher than during type 2 theta. Bland (1986) has reported that the number of discharges during the oscillatory epoch tends to increase linearly with increasing theta frequency in both types of theta (see also Sinclair et al., 1982).

Another important fact is that unit discharges occur during the negative peaks of theta waves. This latter relationship is depicted in more detail in Fig. 12 (Bland, 1985, p.129 or Sinclair et al., 1982) which shows the result of cross-correlating the normalized theta wave and the normalized histogram of the occurrence of unit discharges. As the results of the cross-correlations show, unit discharges occur briefly after (at 216 degrees in Fig. 12) the theta wave has reached its negative peak (at 180 degrees). The finding that the oscillatory epoch is phase related to the theta wave was also reported by several other studies (e.g., Buzsaki et al., 1983; Buzsaki et al., 1992; Fox et al., 1986).

This result does not indicate that every unit discharges during any negative peak of the theta wave. It indicates that in the case a unit is discharging, it is most likely doing so during the negative phase of theta. As Fig. 11 shows unit discharges might be absent during type 2 theta and LIA. This result most likely indicates that field potentials which reflect the summed activity of much larger cell groups are still generated while more local unit discharges at the particular recording sites fail to discharge.

In assuming that behavioral (or task) demands increase from SWS (LIA with very large amplitudes)

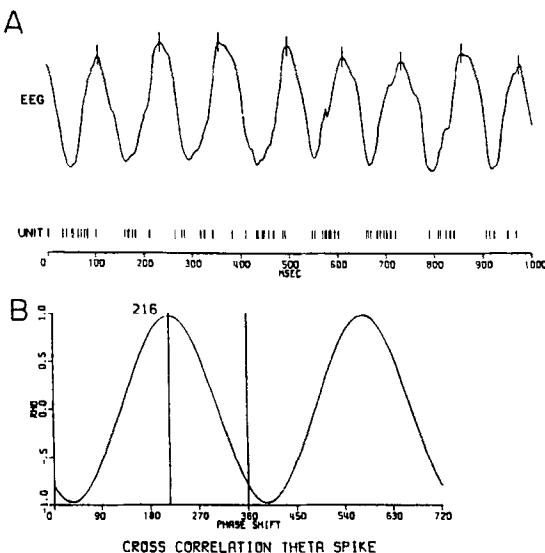


Fig. 12. Theta wave and multi-unit activity converted to a digital event are shown in (A). The result of cross-correlating the normalized theta wave and the normalized histogram of the occurrence of the unit discharges is shown in (B). Degree and direction of correlation is plotted on the ordinate, phase on the abscissa. 180 degrees represents peak negativity. As the results demonstrate, unit discharges occur briefly after the theta wave has reached its negative peak. From Sinclair et al. (1982), reprinted with permission from the authors and the American Physiological Society.

to automatic motor patterns of the LIA type (with smaller amplitudes as compared to SWS) to type 2 theta (perceptual stimulation during immobility) and to type 1 theta behavior (voluntary movements), we arrive at the following interesting conclusions. With increasing task demands (i) during type 1 behavior, the hippocampal EEG synchronizes and becomes more regular showing a dominant rhythmic activity (ii) the frequency of the EEG increases, (iii) the number of discharges during the oscillatory epochs increases, and finally (iv) as compared to SWS the hippocampal EEG desynchronizes outside the range of the theta peak over a broad frequency range. Given these basic findings, it is quite obvious to assume that as a result of increasing task demands, EEG-theta becomes synchronized within the small range of peak theta frequency but desynchronizes in the broad range outside the window of peak frequency (c.f. Leung et al., 1982; Buzsaki et al., 1983). As an example, Dickson et al. (1994) have compared the power spectra for theta (during type 2 behavior)

and LIA. They have found a peak centered at a frequency of 4.25 Hz (type 2, tail pinch evoked theta in anesthetized rats) which was absent in the spectra for LIA (for similar reports see Bland, 1986). Fig. 13 shows a typical example of power spectra during immobility and walking (taken from Lopes da Silva, 1992, p. 84). Comparing the two power spectra clearly reveals that as compared to immobility (bold line), type 1 theta (walk; dotted line) becomes synchronized within a small frequency window.

It has been demonstrated that not only theta power and frequency but theta phase as well is related to behavior. Within the pyramidal cell layer of the rat hippocampus, complex spike cells have been found that unlike theta cells respond with a more irregular pattern of spikes. Because this type of cells responds to the animal's location in the environment, they have been termed place cells (O'Keefe and Dostrovsky, 1971). Place cells fire several bursts of spikes as the rat runs through a particular location in its environment which is called the place field of that cell. In a recent study, O'Keefe and Recce (1993) have found that the interburst frequency of place cells is in the same range as the concurrent EEG-theta (see also the review in O'Keefe, 1993). The most interesting result, however, was that the firing of place cells began at a particular phase of theta frequency as the rat entered the place field. Furthermore, the results indicate that within a particular place field the angle of theta phase is related to a particular spatial location. In other words, if we consider the place field a specific stimulus, theta

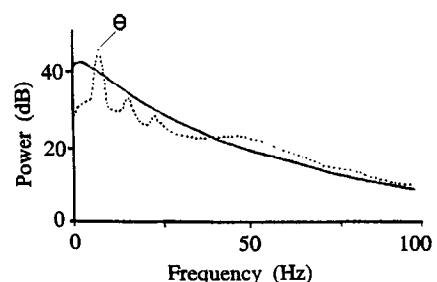


Fig. 13. Schematic power spectrum for ISA or LIA during awake immobility (bold line) and RSA during walking. It is important to see that during walking theta synchronizes within the narrow window of peak frequency, but desynchronizes in adjacent frequency bands outside the theta peak region. As emphasized by Lopes da Silva, the theta peak shows three harmonic components. Modified after Fig. 1 from Lopes da Silva (1992), p. 84.

frequency is phase locked with respect to the appearance of this stimulus.

### 3.3. Memory, hippocampal theta and long-term potentiation (LTP)

Hippocampal LTP is generally considered a synaptic memory mechanism for the encoding of new information. If it can be demonstrated that LTP is related in some specific way to theta, a further argument would be at hand to consider hippocampal theta an important electrophysiological correlate of working memory or episodic memory in particular. In supporting such a relationship the following findings are relevant:

(i) Although LTP has been demonstrated in several brain regions it is most robust and, thus, has been studied most extensively in the hippocampus (c.f. Maren et al., 1994).

(ii) The induction of LTP is optimal with stimulation patterns that mimic theta rhythm (Larson et al., 1986).

(iii) The induction of LTP is dependent on the phase of theta rhythm. It is induced preferentially on the positive phase of the theta rhythm (Pavlides et al., 1988).

(iv) The strength of the induced LTP increases linearly with increasing theta power (Maren et al., 1994; c.f. Fig. 6 on p. 50).

These findings provide strong support for the view that hippocampal theta is related to the encoding of new information, just as LTP is. Thus, it seems likely that theta generally is related to processes in working memory or episodic memory.

### 3.4. Interim conclusions

The most important conclusion is that in response to task demands, hippocampal theta synchronizes in a small frequency window, just as the human theta (scalp) EEG does. Furthermore, hippocampal theta synchronization can be explained in terms of (i) an increase in the duration of multi-unit population bursts and (ii) an increase in rhythmicity of these bursts which have the same frequency as theta.

It is important to note that there are two different forms of theta synchronization. One type of synchronization is related to an increase in power within a narrow frequency band in the range of peak theta frequency. The second form of theta synchronization

refers to ISA (or LIA). This irregular slow activity dominates during SWS and shows an increased power (outside the theta peak range) as compared to immobility and walking (cf. Leung et al., 1982 and Fig. 13). This latter type of synchronization is not related to the increased power of a dominant rhythm within a narrow frequency band, but rather to an increased power over a broad range. It may be explained in terms of irregular oscillatory epochs of the type Buzsaki et al. (1992) have described. Irregular oscillatory epochs occur over a broader frequency range and are not coupled to a 'coordinating' force such as to the regular rhythmicity of a pacemaker. Note, however, that even during irregular synchronization, oscillatory epochs occur synchronously in a large number of cell assemblies and, thus, are related to a rather strong EEG signal showing large amplitude irregular activity.

## 4. Brain oscillations and the EEG: basic concepts and hypotheses

The basic idea proposed in this and the following sections is that memory processes such as encoding, search, spreading activation, and retrieval can be described as a process that modulates the frequency of an oscillatory neuronal discharge pattern (for similar proposals see also Buzsaki et al., 1994 and Lisman and Idiart, 1995). For sensory information processing it is well established that it is the modulation of the frequency of action potentials that encodes the information of a sensory input. A similar way of encoding may also underlie cortical information processing. It is suggested that the modulation of the frequency of brain oscillations reflects basic mechanisms of information transmission in the cortex.

Large changes in oscillatory discharges may be detected in terms of EEG synchronization and desynchronization. However, the fact that synchronization may have different meanings for different frequency bands raises the question whether there is a general meaning for synchronization or desynchronization.

### 4.1. The functional meaning of EEG synchronization and desynchronization

The fact that in response to task demands alpha desynchronizes, whereas theta synchronizes seems to

imply that desynchronization and synchronization have radically different meanings. In this section it will be argued that a special form of synchronization seems to be generally related to the processing of information. The crucial question is here, in which way different subpopulations of cell assemblies are behaving with respect to each other.

As we have shown in sections 2 and 3 alpha synchronizes during mental inactivity. The fact that a strong rhythm, such as the alpha rhythm, can be recorded from scalp electrodes means that millions of cortical neurons must oscillate synchronously with the same phase and within a comparatively narrow frequency band. We have assumed that during desynchronization, different oscillators within the alpha band are no longer coupled. They oscillate with different frequencies. However, it is important to note that within each alpha subpopulation all neurons may still show a regular pattern of synchronous oscillation. This basic EEG-phenomenon of synchronization (during mental inactivity) and desynchronization (during mental activity) provides us with a preliminary but nonetheless important understanding of how information may be processed in the brain: The synchronization of very large populations of neurons oscillating with the same phase and frequency reflects a state in which no information is transmitted.

#### *4.1.1. Different types of synchronization*

In contrast to these classical findings within the EEG alpha frequency range, more recent research with microelectrodes implanted in the cortex, have shown that synchronous oscillatory discharge patterns in high frequency bands (such as the broad gamma band from 30 – 70 Hz) are related to rather localized cortical processes reflecting cognitive activity such as for example, visual encoding processes (e.g., Gray and Singer, 1987). Only at the first glance these two different meanings of neuronal synchronization seem to contradict each other. From the standpoint of EEG research, it is a matter for resolution whether or not we may speak of synchronization or desynchronization. Desynchronization of the EEG is interpreted in terms of frequency and/or phase shifts of a large population of oscillators that become progressively uncoupled. Thus, recorded from EEG macroelectrodes, neuronal activity ap-

pears desynchronized. Nonetheless, however, within small cortical areas, neuronal activity may still exhibit a regular synchronous discharge pattern. To avoid confusions, we will call the synchronous activity of large cortical areas reflecting mental inactivity type 1 synchronization. With type 2 synchronization we denote the regular synchronous oscillatory discharge pattern of selected and comparatively small cortical areas. Type 1 synchronization, reflecting the summed activity of a large number of cell assemblies is a strong signal that can easily be recorded by macroelectrodes from the scalp. In contrast, the synchronous discharge of a small number of cell assemblies is a very weak signal for the human scalp EEG. As a consequence, type 2 synchronization can, therefore, be best detected by microelectrodes but may be difficult or even impossible to detect with EEG macroelectrodes attached to the scalp. Thus, type 1 and type 2 synchronization can be differentiated by referring to the macro- and microlevel of recording respectively.

Within the alpha band, a frequency change within different cell assemblies reflects the processing of information (see also Section 4.2). Because information processing generally is considered a distributed process, a great number of different, distributed cell assemblies will show type 2 synchronization on the microscale in response to cognitive demands. On the macroscale, however, the behavior of many different cell assemblies responding with type 2 synchronization will show up as desynchronization in the EEG. The main reason for this is that each cell assembly will respond with its own frequency and that this synchronization may not be coupled between cell assemblies. Thus, if many different cell assemblies show uncoupled type 2 synchronization, the EEG will be de-synchronized. However, depending on the size of cortical areas exhibiting coupled type 2 synchronization, this type of synchronization may be detected with EEG macroelectrodes as a rather weak signal. In contrast, type 1 synchronization is a very strong signal for the EEG, showing the synchronous, phase coupled oscillatory discharge pattern within a narrow frequency band of very large cell populations.

EEG frequencies are conventionally subdivided in frequency bands such as the theta (4–8 Hz), alpha (8–13 Hz), beta (14 to about 30 Hz) and the gamma

band (30–70 Hz). It is important to note that the traditional terms of EEG (type 1) synchronization and desynchronization apply for the alpha and beta band only. The gamma band seems to synchronize in response to cognitive demands (Pfurtscheller et al., 1994) and seems to reflect real type 2 synchronization in the EEG (see Pulvermueller et al., 1994).

Similarly to the gamma band, the theta band also clearly synchronizes in response to cognitive demands. However, in the human EEG of awake adults, theta is a weak rhythm that most likely is induced into the cortex via a small but distributed set of longitudinal hippocampo-cortical pathways (see section 5.4 below and the review in Lopes da Silva, 1992). In awake adults, theta synchronization seems to denote type 2 regular (rhythmic) synchronization. This sort of synchronization is explained in terms of a small subset of hippocampo-cortical feedback loops responding to an appropriate event or signal with synchronized phase locked theta activity. As a result, selected and distributed cortical cell assemblies may start to respond with synchronous regular theta activity. Accordingly, this type of theta synchronization (RSA in animals) which is related to mental activity shows up as a peak in spectral analysis. On the other hand, however, it is well known that during certain sleep stages, (irregular) theta becomes a dominant frequency even in the human EEG. From animal research it is known that ISA (or LIA) appears in slow wave sleep and that ISA is characterized by larger amplitudes than RSA. Furthermore, as Leung (1980) has shown, only during RSA but not during ISA, theta is in a rhythmic synchronous oscillatory mode. Thus, during sleep, we see a phenomenon which we will term irregular type 1 synchronization. A great number of large cell assemblies oscillate synchronously (hence the term type 1 synchronization) but with an irregular pattern of oscillatory discharges that occur over a broader frequency range.

In summarizing the proposed conceptual framework, we have to distinguish two pairs of different terms: Type 1 and type 2 synchronization referring basically (but not exclusively) to the macro- and micro-level of recording and regular versus irregular synchronization referring to the pattern of synchronous discharges (oscillatory epochs). The term 'regular' thereby means that discharges do not occur randomly but are coupled to some sort of mecha-

nisms that modulates the frequency of discharges in a particular way. The best known example, would be the coordinating force of a pacemaker which increases or decreases frequency and/or the strength of the synchronous discharge pattern. This latter fact could be observed explicitly with hippocampal theta (see Section 4.2). As the results reported by Bland (1986) and other researchers have shown, the duration of the oscillatory epochs and, thus, the strength of the EEG signal increases with increasing frequency and with increasing task demands. This clearly is an example of the modulation of a brain oscillation with respect to task demands.

The behavior of the alpha rhythm can be explained by the terms type 1 (regular) synchronization reflecting mental inactivity and type 2 (regular) synchronization reflecting mental activity. The behavior of the theta rhythm, on the other hand can be described by type 2 regular synchronization (reflecting mental activity) and by type 1 irregular synchronization (reflecting mental inactivity).

The conclusion is, thus, that regular type 2 synchronization is that specific oscillatory mode in all of the frequency bands that reflects actual information processing in the brain. However, despite this similarity in the type of electrophysiological response, it is of crucial importance to note that with respect to the neuronal structures that are involved in the processing of information, an important difference between regular type 2 synchronization in the alpha and theta is to be assumed. For the alpha band we assume that a very large number of cell assemblies in different cortical regions show type 2 synchronization. Due to the structural differences of these different assemblies, frequencies will vary over the entire range of the alpha band. In section 5.3. below we will argue that this type of synchronization provides an ideal framework for describing spreading activation processes in LTM. For the theta band, however, we assume that cortico-hippocampal pathways induce a synchronous oscillation within a narrow frequency window (just within the theta peak) into selected and distributed assemblies in the cortex, thereby binding different parts of cell assemblies together. In Section 5.4 below we will argue that by inducing a regular synchronous discharge pattern into selected cell assemblies, the hippocampus might be able to bind different cell assemblies together.

Thus, in the alpha band, type 2 synchronization refers to the activity of a large number of different assemblies, each assembly oscillating with a different frequency within the alpha band. In contrast, in the theta band, type 2 synchronization refers to the frequency of different parts of only one (although very distributed and large) neuronal structure that is functionally tied together by regular synchronous theta bursts. Table 2 gives an overview over the different meanings of the proposed concepts with respect to the traditional meanings of synchronization and desynchronization.

#### 4.2. Are oscillations mandatory for cortical information processing?

Braitenberg and his coworkers have shown that some of the conventional ideas about the anatomy of the cortex are wrong (see the comprehensive review in Braitenberg and Schüz, 1991). The question he and his group is addressing refers to the issue of specificity or randomness of neuronal connections in

the cortex. They could demonstrate that the probability for an axonal synapse to have a particular neuron as postsynaptic partner is  $p = 0.001$ . The probability that more than one contact is made with a particular cell is extremely small (e.g., for three contacts the probability is  $p = 0.0000001$ ). Given this enormous divergence in interconnectedness, one cell could never selectively excite any other neuron. Due to the principle of temporal and spatial summation (summarized, for example, in Koestner, 1985), a single cell will respond with an outgoing signal (an action potential) only, if many convergent inputs are received at the same time (within a narrow time window). This means that converging neuronal signals must arrive synchronously in order to trigger an outgoing signal. There is, thus, no doubt that a synchronous input is obligatory for a nerve cell to respond. But what are the mechanisms that allow a large number of cells to send synchronous signals?

In considering the fact that a cortical pyramidal cell has about 8000 dendritic synapses (each of which is, on the average, served by a different nerve

Table 2  
The possible meaning of synchronization and desynchronization in the theta and alpha band

Theta			
Traditional terms	Synchronization	Desynchronization	
	ISA or LIA during SWS	RSA	ISA or LIA not during SWS
Proposed terms (see text)	Type 1 irregular syn.	Type 2 regular syn.	Type 2 irregular syn.
EEG band power	increasing in broad theta band	increasing in small window of theta peak	decreasing in broad theta band
Physiological meaning	Large number of cell assemblies irregularly synchronized	Single but distributed cell assemblies synchronized	Small number of cell assemblies irregularly synchronized
Functional meaning	Non-selective activation, Sleep, WMS not active	Selective activation of WMS: BINDING	Non-selective activation of WMS
Alpha			
Traditional terms	Synchronization	Desynchronization	
Proposed terms (see text)	Type 1 regular synchronization	Type 2 regular synchronization	
EEG band power	Increasing in small window of alpha peak	Decreasing over the entire band	
Physiological meaning	Large number of cell assemblies synchronized	Large number of cell assemblies oscillate with different frequencies	
Functional meaning	Inhibition: rest, drowsiness	Spreading activation. Selective activation of information in LTM	

Note: The terms type 1 and type 2 synchronization refer only to processes occurring between different cell assemblies. WMS, working memory system; LTM, long-term memory; SWS, slow wave sleep; syn., synchronization.

cell) a large number of signals will by chance arrive synchronously. Thus, a special mechanism for synchronization must be postulated that goes beyond this background level of random synchronization. There may be many different types of mechanisms that operate to synchronize the neuronal input. However, it appears safe to argue that an oscillatory input is the best possible case to synchronize the neural input for a nerve cell (or even a neural network). When keeping in mind that oscillations consist of rhythmic bursts of action potentials, the reasons for this argument are: (i) The bursts of an oscillatory epoch allow for a fast temporal summation of postsynaptic potentials (The intraburst frequency of an oscillatory event determines the speed of temporal summation). (ii) Temporal summation between different synaptic inputs no longer depends on the exact timing of action potentials but on the interburst period which provides a much larger time window for temporal summation. (iii) If a mechanism like a pacemaker synchronizes oscillations between nerve cells, even in a randomly wired network all or most of the inputs of different nerve cells will be synchronized. Thus, a pacemaker or other mechanisms such as endogenous membrane properties of individual cells (e.g., the reviews in Steriade et al., 1990 and Basar and Bullock, 1992) will maximize the effect of spatial summation. Finally, it is interesting to note that mathematical analyses indicate that particularly in biological systems, oscillators tend to synchronize, if their frequencies are not too different from each other (Strogatz and Stewart, 1993).

Empirical evidence for the synchronizing force of oscillations comes from an interesting study of Buzsaki et al. (1992). In this study it was found that during the oscillatory period the probability of spike bursts stemming from other neurons is three to eight times higher than in comparable time periods in which no oscillatory epochs were observed. It thus seems likely to assume that oscillatory epochs increase the number of synchronous inputs to neighbouring cell groups, thus, increasing their likelihood to respond with a neuronal discharge.

## 5. The proposed model

In this section a ‘model’, or more precisely, a theoretical framework for describing memory pro-

cesses will be discussed that refers to three different levels: (i) the cognitive, (ii) anatomical, and (iii) neuronal or electrophysiological level. The aim, is to describe memory processes in terms of brain oscillations. Thereby an attempt is made to link empirical evidence from divergent fields such as cognitive psychology, neuropsychology, neuroanatomy and electrophysiology. Each of the three levels will be described in a separate subsection below. Arguments connecting the different levels will be discussed throughout the following sections. In an attempt to provide an overview of our arguments, Table 3 shows the basic structure of the proposed model.

### 5.1. The cognitive level of the proposed model

Three basic aspects of memory processes will be distinguished. The first aspect refers to a close interaction between the working memory system (WMS) with the long-term memory system (LTMS). This interaction plays an important role for encoding, searching, retrieving and recognizing information. The second aspect refers to the meaning of monitoring processes which operate under voluntary control within WMS and serve to encode and retrieve information from memory (STM as well as LTM). The third aspect refers to control processes which guide the access and retrieval (but not the search) of information in LTM. The reason to focus on these three aspects of memory is given by the fact that probably any cognitive process depends on the resources of both systems, the WMS and LTMS and on both types of processes, monitoring as well as control processes.

When explaining the model shown in Fig. 14, let us consider a fundamental cognitive process such as recognizing a familiar object. The crucial idea here is that after a sensory code is established, semantic information in long-term memory (LTM) is accessed which is used to identify the perceived object. If the matching process yields a positive result, the object is recognized which in turn leads to the creation of a short-term memory (STM) code. In this case pathways are activated which are similar or identical to those which would serve to retrieve information from LTM (cf. the dashed arrows leading from LTM to STM). This classical explanation of encoding in cognitive psychology, which still reflects the current view, was already stated explicitly by Shiffrin and

**Table 3**  
Overview of the structure of the proposed model

The long-term memory system (LTMS)		
Level	Central issues	Linking arguments
(1) Cognitive	Access into LTM, search and retrieval	A monitoring network is mapped onto a storage network
(2) Anatomy, neuro-psychology	Thalamo-cortical projections; cortical structure	The thalamo-cortical network is mapped onto the cortical storage network
(3) Neuronal structure	Thalamo-cortical feedback loops; structure of cortical codes	The thalamo-cortical network provides access and retrieval; Spreading activation occurs in cortical network
(4) Oscillation	Alpha and higher frequencies	Type 2 synchronization in alpha and higher frequencies reflects the processing of information in the thalamo-cortical and cortical network

The working memory system (WMS)		
Level	Central issues	Linking arguments
(1) Cognitive	Episodic encoding,encoding of new information	New information is attached to existing information in LTM
(2) Anatomy, neuro-psychology	Hippocampo-cortical projections and cortical structure	The hippocampo-cortical network is mapped onto the cortical storage network
(3) Neuronal structure	Hippocampo-cortical feedback loops; structure of STM codes in cortex	Selective activation of the hippocampo-cortical network binds different cortical cell assemblies together
(4) Oscillation	Theta	Type 2 synchronization in the theta band reflects the hippocampal binding process

Geissler (1973): "The process of encoding is essentially one of recognition: the appropriate image or feature is contacted in LTM and then placed (i.e., copied) in STM" (p. 55). It is important to note that the outcome of the matching process does not only depend on the similarity between the sensory code and the appropriate image (prototype, schema or template) held in LTM but on expectancy, selective attention and the level of arousal as well. Top-down processes which are guided by expectancy and selective attention are capable of directing the matching process towards a certain outcome by preactivating or preselecting appropriate templates or prototypes in LTM. These top down processes follow pathways that are similar or identical to those used for accessing LTM (cf. the dashdotted arrows). More recent models, such as Grossberg's adaptive resonance theory (ART), proceed also from the basic assumption that templates or prototypes stored in LTM are activated during a matching process which is characterized by a close interaction between STM and LTM (e.g., Grossberg, 1980; Grossberg and Stone, 1986;

Carpenter and Grossberg, 1993). Complex cognitive processes such as speaking and thinking may also be described in terms of a close interaction between STM and LTM. The basic difference from the foregoing example is that a sensory code is lacking and that a code is generated in STM which in the case of speaking represents a 'plan' of what to say. The codes generated in STM trigger search processes in LTM to retrieve the relevant knowledge about the appropriate semantic, syntactic and articulatory information. This latter idea is similar to Baddeley's concept of working memory, which comprises an attentional controller, the central executive and subsidiary slave systems (Baddeley, 1984; Baddeley, 1992). Within the framework of the present model the concept of a short-term memory system is used in a very broad sense. Thus, the term 'working memory system' (WMS) is adopted to avoid confusion with Baddeley's approach.

Search and retrieval processes in LTM are automatic processes that do not draw on the capacity of STM or the WMS respectively. They are initiated

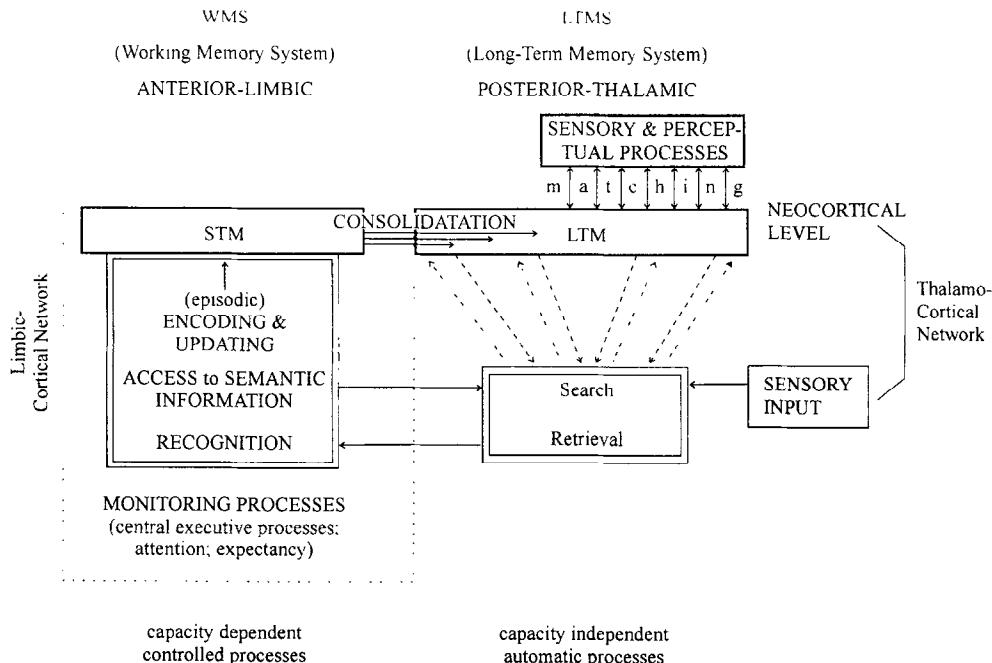


Fig. 14. Two large memory systems, an anterior limbic and a posterior thalamic system are postulated. It is assumed that the anterior limbic system operates on the basis of theta oscillations, whereas the posterior thalamic systems operate on the basis of alpha oscillations. STM and LTM codes are assumed to be stored in the neocortex. Access and retrieval of cortical codes are provided by hippocampo-cortical and thalamo-cortical feedbackloops which converge in particular brain areas that serve as 'monitoring' or 'control' units.

within WMS, but only the result of these processes is fed back to STM. However, initiating a search process requires selective attention and its outcome is evaluated on the basis of expectancy. Both, selective attention and expectancy draw on the limited capacity of STM. Capacity dependent versus automatic processes are, thus, distinctive features between the WMS and LTMS.

Note that encoding has two different meanings. The encoding of sensory information (as a process of recognition) aims at the semantic understanding of perceived information. LTM holds that information which is essential for this encoding process. Within the framework of STM encoding means the creation of a new code that primarily comprises episodic information. According to Tulving (e.g., Tulving, 1984), episodic information is that type of contextual information which keeps an individual autobiographically oriented within space and time. In contrast to a sensory code which primarily reflects physical information, an episodic code which is created through

the action of monitoring processes (cf. the dotted box in Fig. 14) reflects primarily subjective information, such as context, expectancy, emotion and certain autobiographic aspects. Because time changes the context permanently, there is a permanent and vital need to update and store episodic information.

### 5.2. The level of anatomy and neuropsychology

The updating of episodic information may be accomplished by binding different and very heterogeneous aspects such as contextual, autobiographic, emotional and semantic information together. This binding process is understood as an integral part of monitoring processes that result in the formation of a new STM code.

It is interesting to see that the impairment in the consolidation of STM codes appears as the crucial symptom in amnesia which is related to impairments of the medial temporal lobe and the hippocampal formation in particular. In an attempt to explain

consolidation, let us start to consider the formation of STM codes, thereby applying a similar idea we used for perceptual encoding. We assume that LTM information which is searched and retrieved from STM is used to create a STM code. Thus, in a similar way as for perception, different LTM codes (templates, schemata or prototypes) are used as building blocks for the encoding of new (episodic or semantic) information, which basically means some sort of 'restructuring' of known information (Grossberg, 1980). With respect to this view, consolidation can be understood as the maintainance of a binding process that comprises the following aspects, (i) the use and restructuring of already existing LTM information to form a new code, and (ii) the establishment of traces which allow to distinguish the new code from already existing and corresponding LTM information. This latter step also implies the need to establish new search and retrieval pathways (cf. the dashed and dash-dotted lines within LTM in Fig. 14). These pathways are considered as feedback loops that may be used in consolidating new memory traces by maintaining a state of reverberation which allows strengthening of synaptic transmission in a particular cell assembly representing the new code. In a similar way, if these pathways are actually used in retrieving information, the respective cell assemblies are activated and the consolidation process is enhanced.

The proposed explanation of consolidation bears some similarity to the hippocampal indexing theory of Teyler and DiScenna (1986) who assume that the hippocampus stores at least initially some sort of index pointing towards those neocortical modules (representing LTM information) that have been activated. In an interesting theory, Miller (1991) proposes that the hippocampus is important for contextual representations and might be involved in forming global cell assemblies. Squire (1992) emphasizes the 'binding' function of the hippocampus and emphasizes that it is needed to bind together distributed cell assemblies that together represent information of a single code. If the hippocampal formation is involved in the process of consolidation, contextual encoding and binding, thereby using LTM codes which are stored in the neocortex, we have to expect that extensive and widespread projections exist to the association cortices. This is indeed the case (cf.

Lopes da Silva et al., 1990 and the review in Miller, 1991).

While keeping in mind that consolidation is not only relevant to the establishment of more permanent memory traces but also to the formation of new retrieval pathways, the model in Fig. 14 can easily explain the typical amnesic syndrome. Impairment of the hippocampus primarily will impair consolidation and retrieval of new memory codes. This view could also explain why amnestic patients perform quite well in implicit memory tasks, in which they do not attempt to retrieve information (bold arrows between STM and LTM) but instead perform e.g., a word completion test (Graf et al., 1984). In this case patients can use the search and retrieval pathways for semantic LTM information (dashed and dash-dotted arrows) and find the words of the study list because they were activated during the matching process (vertical arrows between LTM and perceptual processes) and as a consequence of this are more easily accessible. The nature of this implicit memory effect may be similar to speeded reaction times in priming experiments, where a primed item can be retrieved faster than an unprimed item. Similar arguments were already proposed by Warrington and Weiskrantz (1968).

Comparing anterograde with retrograde amnesia reveals that in cases where the hippocampal formation is damaged, the anterograde aspect seems to predominate, whereas in cases where regions in the diencephalon (particularly the thalamus) are damaged (such as in Korsakoff's syndrome), the retrograde aspect seems to dominate (e.g., the reviews in Markowitsch, 1984; Markowitsch and Pritzel, 1985; Parkin, 1984). In a more theoretical sense, the anterograde aspect is related to consolidation whereas the retrograde aspect is more related to retrieval. Thus, the diencephalic system may be more related to retrieval processes, whereas the limbic-hippocampal system may be more related to consolidation. This preliminary evidence seems to support the notion that there are two major systems, such as an anterior limbic and a posterior thalamic (or diencephalic) system which is suggested by the model in Fig. 14.

However, many authors focusing primarily on amnesia research suggest that there is no clear evidence to distinguish between a limbic and dien-

cephalic system (e.g., Squire et al., 1993). We assume that these negative findings are due to the fact that by its very nature the WMS and LTMS have to interact closely and that a lesion in one system inevitably impairs functions of the other system. Studies with normal subjects, using e.g., electrophysiological or other functional measures do provide evidence for different anatomical regions of the WMS and LTMS (c.f. the results reported in section 2 and 3).

With respect to the neuronal and electrophysiological level, the general conclusion is that monitoring and control processes represent radically different classes of cognitive processes. Monitoring processes are confronted with what is now termed the binding problem. It refers to the question of how different cell assemblies (or different parts of it) can be tied together to form a new STM code. We will argue in the next following section that theta synchronization, reverberation and LTP are the basic electrophysiological mechanisms that reflect monitoring processes or binding in particular. Control processes operate in LTM and refer to the access and retrieval of the sought-after, relevant information. This type of processes is confronted with what may be termed the 'memory speed effect'. Despite its enormous complexity, LTM must provide mechanisms which enable a fast search for the relevant information. It is of crucial importance to note that the speed of search processes must not be slowed down by the complexity of information stored in LTM. Based on the results, reported in section 2, we assume that alpha frequency and alpha desynchronization reflect processes in the LTMS. Because there is evidence that alpha frequency is related to oscillations in thalamocortical feedback loops (Steriade et al., 1990; Semba et al., 1980), we may assume that the posterior thalamic system is the anatomical basis for the LTMS.

### *5.3. The neuronal and electrophysiological level for LTM*

It is assumed that LTM codes are represented by widely distributed codes which establish a complex network in the neocortex. Even a single code is considered to consist of a structure of features that may be widely distributed throughout different re-

gions of the neocortex. Features may be represented by smaller cell assemblies such as cortical columns or modules which serve as feature detectors when activated by perceptual processes (cf. the close interaction between LTM and perception in Fig. 14). The assumption of highly distributed codes may explain why any attempt to localize a particular engram resulted in a failure (c.f. Lashley, 1950). This structural assumption leads to the crucial question of how the different features belonging to a single code can be activated together as a functional unity without activating features of other overlapping but irrelevant codes. According to the traditional view as first proposed by Hebb (e.g., Hebb, 1949), one may assume that the features of a code are represented by a cell assembly of interconnected cells that are functionally characterized by a concurrent elevation of their average firing rate. Unlike more recent models, Hebb's conception has the disadvantage that in a particular cortical region and within a given time span, only a single code or feature can be activated because the enhanced firing rate is the only cue which allows distinction of the relevant code from irrelevant information. During a search process in LTM, a huge variety of codes will be activated at the same time and possibly in the same brain region. Thus, different and topographically overlapping cell assemblies will be activated at the same time. Consequently, it will be impossible to distinguish between different codes. In an attempt to avoid this problem it may be suggested that assemblies may be functionally defined by a state of synchronous firing of cortical neurons, rather than by an enhanced average firing rate. This means that in a particular cortical region and within a given time span all of the cells may be highly active, but that only those cells firing synchronously represent the relevant information comprised by a single code.

#### *5.3.1. Encoding means to establish a synchronous oscillation pattern*

Gray and Singer (1987) together with other researchers at the Frankfurt MPI (e.g., Gray et al., 1989; Engel et al., 1992) have provided convincing evidence that a visual code, established through a perceptual process, can be described as a cell assembly which responds with a synchronous oscillatory discharge pattern within a broad frequency range of

about 30 to 70 Hz which is termed gamma band. They assume that the synchronous oscillatory firing pattern of distributed cortical cells reflects a stage of cortical integration in the sense that the information provided by different feature detectors is integrated into a single visual code. This assumption is substantiated by the important finding that even widely distributed but synchronously oscillating cell assemblies fire with zero phase lag. Feedback loops, connecting different cell groups of the cortex, obviously are the means which enable this surprising ability. Oscillations are considered carrier signals for the relevant information which might be encoded by the synchronous modulation of frequencies over a broad range. This appealing concept of cortical encoding explains very well how sensory codes are established through perceptual processes. However, the question which remains to be discussed refers to the way in which encoded information is transferred to other brain regions, such as to a monitoring system (c.f. Fig. 14). This 'read out' problem becomes even more obvious if search processes in LTM are considered.

### 5.3.2. Search processes in LTM and synchronous oscillations

When applying the encoding principle described above to search processes in LTM, the interesting conclusion is that the search process would have to find cell assemblies that are capable of establishing a synchronous oscillatory firing pattern in response to the initiation of a search process. According to this concept, the relevant sought after information would be characterized by a synchronous oscillatory discharge pattern. However, appealing as this concept is, the difficult question to be considered is, whether a search processes is capable of establishing a synchronous oscillatory discharge pattern. Unlike a visual encoding process, where all the relevant information is given simultaneously, during the course of a search process, thousands or millions of different codes will be activated at different times. Each code may respond with a synchronous oscillatory discharge pattern, but what should be the criterion to distinguish the sought after relevant from irrelevant information? Thus, establishing a synchronous oscillatory firing pattern along the search pathway would not allow for a selective retrieval of the relevant

information. This question of how a search process finds the relevant information is called the search problem. But in dealing with search processes, two other problems, the read-out problem and the problem of how a search process is initiated must be considered. Because attempts to explain the search problem depends on theoretical concepts that explain how a search is initiated and the result is read out, we first have to consider these questions.

The initiation and the read out problem are related because some sort of control processes are necessary to guide the initiation of a LTM search, as well as the read-out of the relevant information. Inherent to both problems also is the question whether there is (are) a common center(s) in the brain, where a search process is initiated and where the result of a search process is fed back. With respect to the search for a common control center, we proceed from the idea that a control network must be mapped onto a storage network (cf. the dashed and dash-dotted arrows in Fig. 14). Possible candidates are the hippocampus, the basal ganglia and the thalamus with their widespread projections to the neocortex. Because the hippocampus is involved in processes of the WMS and because the basal ganglia seem to play an important role for complex movements, the thalamus with its intense projections to virtually all different cortical regions (e.g., Höhl-Abrahao and Creutzfeldt, 1991) appears a plausible candidate for control processes of the LTMS. It is important to see that as compared to the thalamo-cortical network, the cortical network is orders of magnitude denser. Thus, each feedback loop serves a relatively large cortical field which also will be termed 'alpha field'.

To initiate a LTM search requires some vague information of where in the storage network to look for the relevant information. This information could very well be provided by the thalamus (Sillito et al., 1994). Because it would be highly inefficient to search the entire network once a search process is initiated, it is necessary to delimitate the search area. In a theoretical sense, retrieval cues that give a rough description or some details of the relevant information can serve this purpose. In an anatomical sense, the thalamus might be a good candidate for delimiting the search area in the neocortex because the dense thalamo-cortical network may allow direct access to certain parts of the neocortex. Based on the

current context of the WMS, retrieval cues are provided which are placed in the thalamus where they lead to the selective activation of a particular subset of thalamo-cortical pathways, which start the search process in the neocortex. Thereby, specific and unspecific thalamic projections might provide access to specific sensoric or more abstract information, respectively. However, it should also be noted that in contrast to the traditional distinction between specific and unspecific projections, the thalamus shows a much more complex pattern of different types of projections (e.g., Steriade et al., 1990, p. 40).

It is important to note that the search process is understood as spreading activation process in the cortical storage network emanating from different entry points, which were triggered by certain thalamo-cortical pathways. The aim of the search process is to find a common pathway in the storage network, linking different entry points. Only if common pathways can be activated, the search process will terminate with a positive result. The criterion for a positive result is that 'activation' flows back to each entry point which feeds back the outcome of the search via cortico-thalamic pathways to the thalamus and the WMS.

These considerations bring us back to the search problem, i.e., to the question of how an activation process spreads through the cortical network. The concept of spreading activation used here, is based on a quantitative theory termed 'connectivity model', which is described in detail in Klimesch (1994) and which aims to describe those processes that underlie the memory speed effect. Because the ideas of cortical activation put forward here, are directly related to this theory it seems useful to explain some of the basic assumptions and predictions of this theory. The connectivity model describes the flow of activation in abstract terms of different activation values moving from one node to another. In the context of cortical activation the term 'activation value' should be translated into 'frequency of an oscillatory neuronal discharge pattern'. As an example, let us consider an interconnected structure of  $n$  nodes which represents a single code. At the beginning of an activation process each node representing a cell assembly (or cortical module) has zero activity which means that it oscillates with some (comparatively) low frequency. Activating a node means to put it in a

state of oscillation with a frequency that is higher than its resting frequency. Now, if activation starts at some node  $x$  with frequency  $f$ , this activation spreads to all of the other  $n - 1$  nodes of that code. Accordingly, nodes 2, 3, 4 and 5 are also put in oscillation with frequency  $f$ . Now, in a second activation stage, the  $n - 1$  nodes activate each other. Thus, each node receives activation from the remaining  $n - 2$  nodes. With each additional activation, the  $n - 1$  nodes increase their responsiveness which means that they increase their frequency proportional to the number of times they were activated. Note that all of the  $n - 1$  nodes are completely interconnected and are, thus,  $n - 2$  times activated which results in an increase in frequency from  $f$  to  $f'$ . In a third step, the increased frequency  $f'$  is fed back to  $x$ , i.e. to the node where the activation process was initiated. Note that the increase from  $f$  to  $f'$  reflects the complexity of a code. The more nodes there are, the higher frequency  $f'$  and consequently, the faster the spreading activation process will be. Furthermore, due to the interconnections between the  $n - 1$  nodes, which are considered the features of a code, a synchronous oscillatory discharge pattern is established within all of the components of a code. Thus, in accordance with the findings of Gray and Singer (1987), a memory code can be characterized by a pattern of features oscillating synchronously (see also Gray, 1994 for a more recent review). However, during the spreading activation process, each code is activated at a different time and even more important, each code will respond with a different frequency, because frequency  $f'$  depends on geometric properties which differ between codes.

According to the connectivity model, a search process terminates with a positive result if activation (i.e., some frequency  $f'$  which must be higher than input frequency  $f$ ) spreads back as 'echo' to one of those nodes where the search was initiated. Complex control processes do not guide the spreading activation which follows automatically by local mechanisms. Their task is to select access points, when initiating a search process, and to retrieve the relevant information if a search process terminates with a positive result. The result of a search process can be judged by the strength of activation equalling frequency  $f'$  of activated codes. That code responding with the highest frequency represents the rele-

vant information to be retrieved. The mechanisms that identify the relevant code(s) cannot be explained by the spreading activation processes per se, but only by a special control system.

In the identification of the relevant nodes or codes, feedback loops may play a decisive role. During the course of a search process the activation status of the searched network is constantly transmitted back by means of feedback loops to a control system which is located in the thalamus. The basic idea underlying this process is already outlined in the right part of Fig. 14. Thalamo-cortical feedback loops connect the thalamus with the cortical neural network. As compared to the thalamo-cortical network, the cortical network is orders of magnitude denser. Thus, each feedback loop serves a relatively large cortical field which also oscillates within the alpha frequency range. These cortical fields will be termed 'alpha fields'.

### *5.3.3. The two alpha bands, control and search processes*

When considering the question, which of the two alpha bands is relevant for search processes in LTM, it is important to keep in mind that we are confronted with a complex structure in which one network (the thalamo-cortical) is mapped onto another network (the cortical storage network). Thus, the question arises, whether the two alpha bands are related to these two different types of networks. Because our results indicate that the upper alpha band reflects semantic LTM processes (c.f. section 2.4.2.), it is obvious to assume that upper alpha band oscillations are (besides oscillations in the beta and gamma band) related to processes in the cortical storage network. The lower alpha band, on the other hand, was found to reflect attentional processes. Therefore, it seems plausible to hypothesize that the lower alpha band reflects control processes which are related to oscillations in thalamo-cortical feedback loops. Because these feed-back loops serve a particular field in the cortex, which was termed alpha field, the result of the spreading activation process within each alpha field can be fed back to the thalamus.

According to this view, we can distinguish between a cortical and subcortical level of alpha activity. There not only is experimental evidence for this

view (Lopes da Silva et al., 1973 and Hogan and Fitzpatrick, 1987), the fact that alpha is a dominant rhythm in the scalp EEG also strongly supports the view that alpha also must have a cortical origin.

Finally, it is important to recall the findings of Gray and Singer which show that synchronous oscillations in a much higher frequency range than alpha is related to cortical encoding processes. We may assume that comparatively small cell assemblies such as cortical columns (representing sensory information) oscillate within the gamma frequency range, whereas large assemblies (representing semantic information) oscillate within the alpha frequency range. However, if this would be true it would be necessary to postulate some sort of transition or interface between alpha and gamma oscillations. The following two facts support this idea. First, Steriade et al., 1990, (p. 147) report that the gamma rhythm (the 40 Hz rhythm in particular) is driven by neurons located in that cortical layer which receives thalamic afferents. They conclude that thalamic input to the cortex serves as a trigger for rhythmic activation of specific cortical columns. Second, Pfurtscheller et al. (1994) observed a reciprocal relationship between alpha and the 40 Hz rhythm: If the 40 Hz rhythm synchronizes, alpha desynchronizes and vice versa.

### *5.3.4. Type 1 versus type 2 synchronization, spreading deactivation versus spreading activation*

Type 1 synchronization of large cell populations is considered to reflect a state of inhibition. With respect to search processes in LTM, type 1 synchronization may reflect the inhibition of irrelevant information which also may be called 'spreading deactivation.' As an example, at the beginning of a search process, large cortical areas may oscillate synchronously with resting frequency  $f$ . Because information is encoded by the modulation of frequencies, large cell populations oscillating with the same (low resting) frequency are not capable of transmitting information. However, as a result of a search (or spreading activation) process, different cortical cell assemblies change their frequency and establish a pattern of type 2 synchronous oscillatory process. This modulation or change in frequency reflects the process of transmitting information but is restricted to those cortical areas that are relevant for a search process. The fact that during desynchronization a

complex pattern of changes in EEG coherences can be found, as the interesting work of Petsche and his group demonstrates (e.g., Petsche and Rappelsberger, 1992) is well in line with the proposed interpretation.

The significance of type 1 synchronization for memory processes becomes evident when considering the fundamental question of how it can be explained that spreading activation is confined to the relevant parts of the (cortical) memory network (Klimesch, 1994). The most obvious way of handling this problem is to assume strong inhibitory processes that allow a search process to spread only within certain regions of the network. According to Braitenberg and Schüz (1991), however, the assumption of powerful inhibitory processes is not plausible, given the fact that about 85% of all cortical neurons are pyramidal cells with excitatory synapses. Inhibitory synapses are comparatively rare (comprising only 11 to 15% of all cortical synapses) and reside on stellate cells that primarily make local connections. Thus, in the cortical network, inhibitory processes are more likely operating locally and probably do not have far reaching effects. Type 1 synchronization, induced in large areas or even in the entire cortex (e.g., during the initiation of sleep) may have powerful inhibitory effects. When type 1 synchronization is selectively induced in certain cortical areas from a part in the brain that operates as some kind of 'control unit', the basic theoretical framework for explaining inhibitory processes by type 1 synchronization are at hand. According to this idea, type 1 synchronization could act to block a search process from entering irrelevant parts of the network.

### 5.3.5. Empirical evidence: the memory speed effect

The assumptions that memory codes are retrieved via longitudinal pathways linking thalamic nuclei with the cortex, and that alpha is the predominant rhythm reflecting the activity of these pathways have led to the hypothesis that alpha frequency should be related to memory performance. The finding of a positive relationship between memory performance and alpha frequency has provided strong support for this hypothesis (see section 2) and suggests a rather general significance of the memory speed effect for information processing.

In addition to the finding that good memory performers have a significantly higher alpha fre-

quency than subjects with bad memory performance, behavioral data also have shown that with increasing memory performance retrieval time decreases (Klimesch et al., 1988). It is important to note that a variety of early EEG studies have documented that alpha frequency is negatively correlated with simple reaction time to auditory or visual stimuli (Surwillo, 1961; Surwillo, 1963a; Surwillo, 1963b; Surwillo, 1964b; Woodruff, 1975) but also with decision time in more complex tasks (Surwillo, 1964a). In this latter study, the finding that the correlation between alpha frequency and decision time increases with increasing task complexity has led Surwillo (1964a) to conclude that alpha frequency is a general indicator of the speed of information processing in the brain.

Another finding reflecting a different aspect of the memory speed effect stems from semantic decision tasks in which subjects had to judge natural concepts. In a variety of different experiments (summarized in Klimesch, 1994), it was found that complex concepts can be processed much faster than less complex concepts. It could be demonstrated that this effect is not due to confounded variables such as typicality, word frequency or degree of connectivity.

For cognitive psychology, the fact that more complex information can be processed faster than less complex information is a challenge, because well established theories (such as e.g., the well known ACT\* theory from Anderson, 1983) and related experimental results show the opposite effect. In dealing with this challenge, a new model, the connectivity model of semantic processing was developed (Klimesch, 1987; Klimesch, 1994). According to this model and related experimental findings, the memory speed effect may be considered a general principle for the processing of integrated (interconnected) semantic LTM codes which does not hold true for episodic short-term memory (STM) demands (Kroll and Klimesch, 1992).

The connectivity model explains memory performance in terms of an increase in the speed of the spreading activation process. It, thus, seems plausible to see a possible link with the finding that alpha frequency increases with increasing memory performance. Klimesch (1994) has shown that a theoretical explanation of the memory speed effect requires a particular set of structural and processing assump-

tions. The description of a cortical search process described earlier in this section, is based on these assumptions that also underlie the connectivity model which was suggested by Klimesch (1987); Klimesch (1994).

#### *5.4. The neuronal and electrophysiological level for the WMS*

We propose that monitoring processes and consolidation in particular, are reflected by type 2 synchronization in the theta range. More precisely, it is assumed that type 2 theta synchronization induced in selected hippocampo-neocortical feedback loops actually reflects the more permanent encoding of new (episodic) information. LTP which crucially depends on the strength of synchronized theta will play an important role for a more permanent storage of new information (c.f. the empirical evidence discussed in section 3.3.). Type 2 theta synchronization might also provide the basis for establishing a binding process that functionally links cell assemblies in LTM in a new way, thereby creating contextual information for an encoded event. Carpenter and Grossberg (1993) emphasize a similar view. They assume that the hippocampus represents something like an orienting system that allows for an efficient context related encoding of a new stimulus.

##### *5.4.1. Theta and the selective activation of information*

When trying to explain the possible functional significance of the theta rhythm in the human EEG, we assume that synchronized bursts of a small set of hippocampal pyramidal cells induce theta activity in selected, but distributed cortical regions which are relevant for performing a particular task. As we have emphasized in section 3, empirical findings support this view and indicate that theta band power increases with increasing (episodic) task demands (Klimesch et al., 1994; Klimesch et al., 1996b; Klimesch et al., 1996c; see also Arnolds et al., 1980). Research in animals also indicates that during behavioral activity theta power increases (e.g., the review in Lopes da Silva, 1992).

Evidence for the view that only a small percentage of hippocampo-cortical feedback loops is synchronized comes from a re-examination of the pacemaker role of the septum in the production of the

hippocampal theta rhythm (Petsche et al., 1962; Stewart and Fox, 1990). In addition to cholinergic projections, a large fraction of the septo-hippocampal projections terminate on inhibitory (GABA-ergic) hippocampal interneurons (Freund and Antal, 1988; see also the reviews in Lopes da Silva, 1992 and Stewart and Fox, 1990). Based on these and related findings, Stewart and Fox (1990) assume that the septal input might organize the hippocampal theta activity via rhythmic inhibition of hippocampal interneurons. This view is in agreement with the fact that hippocampal interneurons are more likely to behave as theta cells (Fox and Ranck, 1981) than burst firing pyramidal neurons. In agreement with this fact, a simulation model (Traub et al., 1989) reveals that in contrast to interneurons only a small percentage of the pyramidal cells display synchrony.

The fact that only a small percentage of the pyramidal neurons displays synchrony, agrees with the idea that hippocampo-cortical feedback loops induce synchronous theta activity into selected cortical areas where new information is encoded or freshly information is retrieved. This is type 2 or selective synchronization that means activation. Given the fact that theta frequency induces or at least enhances LTP (see also Lopes da Silva, 1992), it seems tempting to assume that theta activity, induced into selected cortical areas, reflects a process to encode or retrieve new information by keeping or putting selected cortical areas into a state of resonance. This assumption comes very close to a theory of resonant phase-locked hippocampo-cortical loops, proposed by Miller (1991).

##### *5.4.2. Reasons why theta is not a dominant rhythm in the human EEG*

One of the first questions that may arise when considering the proposed hypothesis is, why — in contrast to animals — theta is not a dominant rhythm in the human EEG. In an attempt to answer this question we first proceed from a theoretical consideration that is similar to those that were proposed for accessing and retrieving LTM codes. It is assumed that hippocampo-neocortical feedback loops induce synchronized rhythmic theta activity onto different regions of the neocortex where (e.g., by means of LTP) new information is encoded or freshly encoded information is retrieved. Given the basic assumption

that new information always will be ‘added’ or ‘attached’ to related but already encoded information, only a small subset of the hippocampo-cortical feedback loops which are related to relevant cortical areas will be needed and, thus, will actually show synchronized theta activity. Because the human cortex is much larger than that in lower mammals and, as a consequence, holds much more LTM information, the encoding of new information is a much more distributed process than in animals. Thus, if the percentage of synchronized hippocampo-cortical feedback loops is related to the size of the cortex (and to the hippocampus too, which is relatively much smaller in humans), this percentage will be orders of magnitudes smaller for humans as compared to animals.

With respect to the question whether theta activity can be observed in the human scalp EEG, these findings obtained from microelectrodes in the hippocampus are of outstanding importance. Biophysically, theta frequency in the hippocampus, deep inside the brain, would be difficult to detect from scalp electrodes. The crucial condition to detect theta as a dominant rhythm in the EEG would be that most of the burst firing hippocampal pyramidal cells that project to other parts of the cortex would fire in synchrony. However, as we have already noted, according to Leung (1980), Traub et al. (1989) and Lopes da Silva (1992), this is not the case. And indeed, as judged by visual inspection but in contrast to spectral analysis, theta activity usually is absent in the EEG of normal, awake adults.

#### *5.4.3. Theta, sleep and the encoding of new information*

It has frequently been proposed that during sleep, memories that were acquired during the day are activated or ‘replayed’. In an interesting study, Skaggs and McNaughton (1996) investigated hippocampal place cells in rats during actual behavior and sleep. They have found that the correlated activity of place cells during sleep reflects the activity of those cells during earlier spatial exploration. Most interestingly, as the calculation of cross correlations revealed, during actual behavior place cells show a strong theta frequency modulation which is missing during sleep. This finding provides further support for the view that rhythmic hippocampal theta activity

is related to processes in the WMS. During sleep different memories might well be activated, but the WMS will not be active in a sense that new (or episodic) information will be encoded or that monitoring processes which operate under voluntary control can be carried out. This finding also is in line with the fact that RSA reflects the selective activation of relevant information, whereas ISA (or LIA) reflect the non-selective activation (of some information without a particular context or episodic information) during sleep (see Table 2).

## 6. Theta frequency and event related potentials

A possible objection against the proposed hypothesis that brain oscillations are a basic phenomenon of cortical information processing may come from researchers using event related potentials (ERPs) to study cognitive and memory processes in particular. They may argue that at least late components of ERPs reflect completely different types of cortical processes such as time-locked threshold changes that regulate the degree of excitability in neuronal networks (e.g., Birbaumer and Elbert, 1988; Elbert, 1992). Given the fact that almost all of the memory studies in cognitive electrophysiology focus on late components of ERPs, this objection could seriously threaten the general validity of the proposed hypothesis.

However, it may also be argued that even late components of ERPs are the result of synchronous oscillations that are transiently phase locked in response to a relevant event or stimulus. Summed up over several trials, a waveform (the ERP) would be generated that shows the typical succession of positive and negative ‘peaks’ (or ERP components). If we proceed from this idea it becomes evident that only (or at least primarily) those types of oscillations would be capable of generating late ERP components that indeed respond with increasing synchronization to an increase in respective task demands. Note that alpha and beta tend to desynchronize with increasing task demands. Hypothetically there are only two possible candidates: theta and gamma frequency. Because gamma frequency is much too high and its amplitudes much too small to generate a typical ERP, theta frequency remains the most plausible candidate.

Given the fact that much of the power of ERPs lies in the delta band, this proposal, of course, does not mean that theta is the only generator for ERPs. The argument is just that theta is capable of influencing significantly amplitude and latency measures of ERP components. Weak influences may even be due to type 2 synchronizations within the alpha band.

The most obvious ERP component that might be sensitive to reflect phase-locked evoked theta activity is the P300 for the following two reasons. First, because of the (typical) latency and form of the P300, this ERP component shows significant power in the theta band as frequency decompositions indicate (Basar and Stampfer, 1985). Second, the (typical) functional meaning of the P300, particularly the process of 'updating' (Donchin and Coles, 1988) is well related to central functions of the WMS.

Now, let us consider the most speculative part of the proposed argument that phase locked theta activity is related to the P300 component of ERPs. In keeping in mind that a single cycle of the theta rhythm consists of an inhibitory and a disinhibited or excitatory phase and that only in the latter, bursts of action potentials are sent to selected cortical areas, the question arises with which phase of the cycle task related (episodic) processing starts. Does it start with the inhibitory or the excitatory phase? In referring to the argument that theta is induced in selected parts of the cortical network it seems plausible to assume that episodic processing starts with the inhibitory phase in order to maximize the impact of the distributed synchronized activation of the relevant parts of the network by reducing irrelevant background activity through the inhibitory phase. As a result of this assumption and because only a small percentage of the burst firing pyramidal cells are synchronized through the excitatory phase, the outcome should be a positive going deflection in the EEG, time locked to the presentation of an adequate stimulus.

If this is true, it should be possible to record evoked theta activity from the scalp in response to an appropriate stimulus or event. Based on theoretical considerations and experimental evidence (e.g., Leung, 1980), Lopes da Silva, 1992, (p. 93) concludes that appropriate stimuli or events induce evoked responses that depend on the phase of theta frequency. Thus, evoked theta activity may be viewed

as synchronized phase-locked and thus amplified theta frequency which occurs in response to an appropriate event. The issue of interest thus is, whether evoked or event-related theta activity can be detected as a response to increased episodic memory demands.

It was emphasized that one of the most important functions of the WMS that are related to hippocampal information processing is the encoding of contextual or episodic information. Thus, if some significant proportion of the power of the P300 really stems from phase-locked hippocampal theta activity, the (typical) functional meaning of the P300 should be related to the encoding of contextual and the encoding of new information.

There is some evidence for this view. Donchin's updating hypothesis (e.g., Donchin and Coles, 1988) is one of the best examples. It is well established that the P300 amplitude is related to the degree of contextual encoding (e.g., Donchin and Coles, 1988), expectancy (or subjective probability), and the amount of effort which is also reflected by the amount of information transmitted to a subject (see e.g., Johnson's triarchic model in Johnson, 1986, and the summary in Verleger, 1988; p. 351). It is important to note that Verleger (1988), who is challenging Donchin's updating hypothesis, is not challenging the significance of the P300 with respect to contextual encoding. His argument basically is that the P300 does not reflect the 'updating' but instead the 'closure' of expectancies.

A positive relationship between the P300 and the consolidation of memory codes (as a typical hippocampal function) was demonstrated by some of those studies reporting a Dm effect. Several studies have shown that ERPs recorded during the encoding of words (or pictures) that were later remembered were more positive than ERPs to words (or pictures) that were not remembered (Sanquist et al., 1980; Karis et al., 1984; Johnson et al., 1985; Neville et al., 1986; Fabiani et al., 1986; Paller et al., 1987; Fabiani et al., 1990; Friedman, 1990a, Friedman, 1990b and see also the indirect evidence provided by e.g., Noldy et al., 1990 and the review in Paller, 1993). This difference in ERPs during encoding which was found within the region of the typical P300 or a late positive component was termed 'Dm' (for difference based on later memory performance;

Paller et al., 1987) or Dm effect. When reviewing this research it is interesting to see that, particularly, the P300 does not reflect the processing of semantic information (i.e., the encoding of a stimulus per se) but instead the processing of episodic information. Results reported by Karis et al. (1984) and Fabiani et al. (1986), Fabiani et al. (1990) are in good agreement with this interpretation. They presented subjects with different series of words which had to be recalled immediately after a list was presented and found that words later recalled elicited larger P300s than words not recalled. In addition, Fabiani et al. (1990) were able to demonstrate that this relationship between the P300 amplitude and episodic memory performance holds only, if subjects use rote learning (which is based on the encoding of contextual and thus episodic information) but not if subjects use semantic encoding strategies (such as organizing the words into meaningful sentences). Thus, the Dm (with respect to the P300) most likely reflects episodic encoding processes and as a result, this type of Dm effect which is based on the P300 component becomes the weaker, the more semantic encoding processes predominate.

Electrophysiological recordings with electrodes implanted in the hippocampus have not provided clear evidence for the view that the P300 is generated in the hippocampus (e.g., Polich and Squire, 1993, and the literature reviewed in this article). Because theta is generated in the septum and because other parts of the limbic system also exhibit theta frequency, the crucial question is, whether or not it can be demonstrated that theta activity (or the P300) varies as a function of (episodic) memory performance and that, at the same time, the hippocampus is involved in the modification of theta activity (or the P300).

An interesting study by Smith and Halgren (1989) who focused on the word repetition effect in a recognition task provided evidence for this view. It is well known that old words (repeated words) elicit a larger P300 than new words (e.g., Sanquist et al., 1980 and Johnson et al., 1985). Smith and Halgren (1989) repeated the targets in the recognition task in each of a set of nine blocks of 20 words (consisting of 10 targets and 10 new words) and found that the amplitude difference between repeated and new words did not change with the number of repetitions

(i.e., the number of blocks). Recognition performance, of course, increased with the number of blocks, but this increase of performance was not reflected by the amplitude differences between the repeated and not repeated words which remained constant with the number of repetitions. Because these results were found for normal subjects as well as for patients with unilateral (left or right) anterior temporal lobectomy, it was concluded that the hippocampus is not involved in the increase of recognition performance over different blocks, which can be explained as increase in implicit memory performance. Most important, however, the baseline recognition performance was significantly lower for the patients with a left temporal lobectomy who from the very beginning also failed to show a significant P300 amplitude difference between new and old words. This latter result is consistent with the hypothesis that the hippocampus (in the dominant left hemisphere) might be capable of modifying a P300 that reflects explicit, episodic memory performance.

In an interesting recent study, Knight (1995) reports evidence which shows that the P300 might be related to hippocampal processes. The results of his study document that for hippocampal patients and in contrast to normals, the P300 for complex novel stimuli is missing, while it is preserved in a simple oddball task.

## 7. Concluding remarks

The main purpose of this article is to encourage an integrative and interdisciplinary view on memory processes. As a result of this attempt, new experiments can be performed that will be capable of critically evaluating the proposed hypotheses. A promising empirical approach would be to analyze event-related shifts in EEG power within the theta and alpha band in amnesic subjects who perform different types of memory tasks.

If it is true that oscillations are the mandatory basis for information transmission in the cortex and possibly in the entire brain, a better understanding of the nature of oscillations would be essential for an integrative view in cognitive neuroscience. For cognitive psychology this would mean to finally describe cognitive processes in terms of oscillations and for cognitive psychophysiology this would mean

to focus primarily on the analysis of certain, carefully selected frequency bands in addition to the study of event-related potentials.

### Acknowledgements

This research was supported by the FWF project P-11569.

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