

Full-length review

EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis

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Abstract

Evidence is presented that EEG oscillations in the alpha and theta band reflect cognitive and memory performance in particular. Good performance is related to two types of EEG phenomena (i) a tonic increase in alpha but a decrease in theta power, and (ii) a large phasic (event-related) decrease in alpha but increase in theta, depending on the type of memory demands. Because alpha frequency shows large interindividual differences which are related to age and memory performance, this double dissociation between alpha vs. theta and tonic vs. phasic changes can be observed only if fixed frequency bands are abandoned. It is suggested to adjust the frequency windows of alpha and theta for each subject by using individual alpha frequency as an anchor point. Based on this procedure, a consistent interpretation of a variety of findings is made possible. As an example, in a similar way as brain volume does, upper alpha power increases (but theta power decreases) from early childhood to adulthood, whereas the opposite holds true for the late part of the lifespan. Alpha power is lowered and theta power enhanced in subjects with a variety of different neurological disorders. Furthermore, after sustained wakefulness and during the transition from waking to sleeping when the ability to respond to external stimuli ceases, upper alpha power decreases, whereas theta increases. Event-related changes indicate that the extent of upper alpha desynchronization is positively correlated with (semantic) long-term memory performance, whereas theta synchronization is positively correlated with the ability to encode new information. The reviewed findings are interpreted on the basis of brain oscillations. It is suggested that the encoding of new information is reflected by theta oscillations in hippocampo-cortical feedback loops, whereas search and retrieval processes in (semantic) long-term memory are reflected by upper alpha oscillations in thalamo-cortical feedback loops. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: EEG; ERD; Alpha; Theta; Oscillation; Memory; Hippocampus; Thalamus

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1. Introduction

In a physiological sense, EEG power reflects the number of neurons that discharge synchronously. Because brain volume and the thickness of the cortical layer is positively correlated with intelligence (e.g., Refs. [12,165]) it is tempting to assume that EEG power too, is a measure that reflects the capacity or performance of cortical information processing. Although it will be argued that this is in principle the case, it must be emphasized that power measurements are strongly affected by a variety of unspecific factors such as the thickness of the skull or the volume of cerebrospinal fluid, by methodological and technical factors (such as interelectrode distance or type of montage) but also by more specific factors such as age, arousal and the type of cognitive demands during actual task performance.

It is the purpose of the present article to show that EEG power is indeed related to cognitive and memory performance, but in a complex and partly non-linear way. Within the alpha frequency range EEG power is positively related to cognitive performance and brain maturity, whereas the opposite holds true for the theta frequency range. Alpha and theta reactivity as well as event-related changes in alpha and theta band power show yet another pattern of results. During actual task demands the extent of alpha power suppression is positively correlated with cognitive performance (and memory performance in particular) whereas again the opposite holds true for the theta band. Here, the extent of theta synchronization is related to good performance. The review which focuses on the theta and alpha frequency range considers first tonic changes in power (such as age related differences in the EEG) and then phasic or event-related changes.

1.1. Cognitive and memory performance: introductory remarks

Two basic aspects of memory processes will be distinguished [66]. The first refers to processes of the working memory system (WMS), the second to that of the long-term memory system (LTMS). Probably any cognitive process depends on the resources of both systems. As an example, let us consider an every day cognitive process such as recognizing a familiar object. The basic 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, bottom up pathways are activated which are similar or identical to those which would serve to retrieve information from LTM. This classical explanation of encoding still reflects the current view, which was originally stated by Shiffrin and Geisler [137]: “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). Complex cognitive processes such as speaking and thinking may also be described in terms of a close interaction between the WMS and LTMS. The basic difference to 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 [3,4].

In the WMS, encoding has two different meanings, one refers to episodic, the other to sensory-semantic information. The encoding of sensory information (as a process of recognition) always aims at the semantic understanding of perceived information which is first processed in the LTMS. Because of this close relation between sensory and semantic encoding we will use the term sensory-semantic code. The creation of a new code comprises episodic information, which according to Tulving (e.g., [158]), is that type of contextual information which keeps an individual autobiographically oriented within space and time. Because time changes the autobiographical context permanently, there is a permanent and vital need to update and store episodic information. Thus, the formation of episodic memory traces is one of the most important tasks of the WMS.

Cognitive performance is closely related and linked to the performance of the WMS and LTMS. As an example, most intelligence tests comprise subtests measuring memory span (an important function of the WMS) and tests such as judging analogies (which reflect an important aspect of semantic LTMS). The increase in cognitive performance from childhood to puberty as well as the decrease in performance during the late lifespan is, most likely, due or at least closely linked to performance changes in the WMS and LTMS.

With respect to the functional anatomy of memory, there is good evidence that brain structures that lie in the medial temporal lobe (comprising the hippocampal formation) and prefrontal cortex support various functions of the WMS (cf. the reviews in Refs. [102,140,141] and findings about the contribution of the hippocampal region for the generation of event-related potentials in the human scalp EEG during novelty detection [85,86]). Studies focusing on the ontogeny of human memory indicate that the hippocampus matures relatively early in postnatal life, whereas the prefrontal cortex which is important for the development of an increased memory span matures much later (cf. Refs. [109,57] for reviews). Although many aspects of memory develop early in childhood (up to an age of about 2 or 3 years) it is not yet known when memory is fully matured. As will be discussed in Section 5, there is good evidence that a complex structure of feedbackloops (or ‘reentrant loops’; [37]) connecting the hippocampus with different cortical regions and the prefrontal cortex in particular may provide the anatomical basis for the WMS. It appears likely that these feedbackloops develop and become increasingly differentiated with increasing age over the entire time span of childhood and possibly early adulthood. The increase in EEG frequency during that life period may (besides other factors) reflect this process of brain maturation. The basic assumption is that the better these feedbackloops become integrated and interconnected with other brain areas, the faster the frequency of EEG oscillations will be.

1.2. Alpha and theta: some basic aspects

Alpha is (with the exception of irregular activity in the delta range and below) the dominant frequency in the human scalp EEG of adults. It is manifested by a ‘peak’ in spectral analysis (cf. Fig. 1) and reflects rhythmic ‘alpha waves’ which are known since Berger (e.g., Ref. [10]). The fact that alpha clearly is an oscillatory component of the human EEG has led to a recent ‘renaissance’ in the interest of EEG alpha activity [5,8,7,9].

Frequency and power are closely interrelated measures. Usually, alpha frequency is defined in terms of peak or gravity frequency within the traditional alpha frequency range (f_1 to f_2) of about 7.5–12.5 Hz. Peak frequency is that spectral component within f_1 to f_2 which shows the largest power estimate (cf. Fig. 1A). Alpha frequency can also be calculated in terms of gravity (or ‘mean’) frequency which is the weighted sum of spectral estimates, divided by alpha power: $(\sum(a(f) \times f)) / (\sum a(f))$. Power spectral estimates at frequency f are denoted $a(f)$. The index of summation is in the range of f_1 to f_2 . Particularly if there are multiple peaks in the alpha range (for a classification see e.g., Ref. [39]), gravity frequency appears the more adequate estimate of alpha frequency.

As is well known from animal research, unlike alpha in the human scalp EEG, theta is the dominant rhythm in the

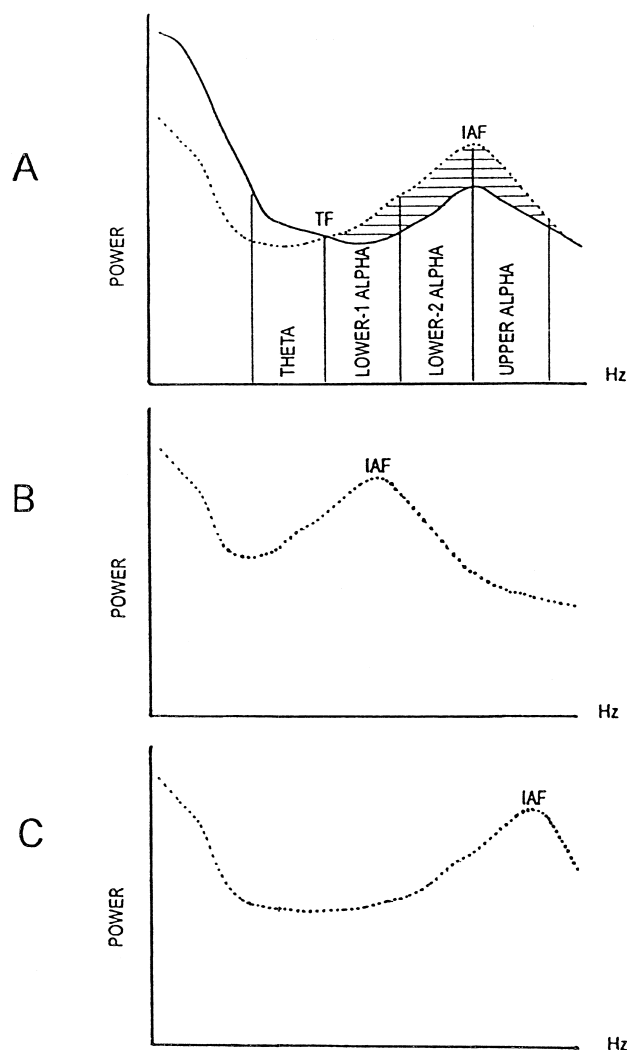


Fig. 1. Individual alpha frequency (IAF) varies to a large extent even in a sample of age matched subjects as the three power spectra indicate. Depending on their memory performance and other factors, IAF lies in the range of about 9.5–11.5 Hz for young healthy adults. (A) If power spectra are calculated separately for a resting period in which subjects are in a state of alert wakefulness (dotted line) and during actual task performance (e.g., memorizing visually presented words), alpha power becomes suppressed, but theta power increases (bold line). That frequency where the two spectra intersect marks the transition frequency (TF) between the theta and alpha band. Experiments from our laboratory have shown that TF lies almost 4 Hz below IAF and that the lower alpha band (which can be further divided in two subbands) is somewhat wider than the upper alpha band. (B) Alpha power of a subject with a very slow alpha rhythm will fall outside the fixed frequency window of the traditional alpha band of about 7.5–12.5 Hz. As an example, if IAF in (A) is 10 Hz and in (B) only 8 Hz, the lower alpha band in (B) will already comprise that frequency range which is the theta band in (A), whereas the upper alpha band in (B) will fall in the frequency range of the lower alpha band in (A). Similar problems arise, if IAF lies already at the upper frequency limit of the alpha band. (C) For a subject with a very fast IAF of about 11.5 Hz or more, almost the entire frequency range of the traditional alpha band (7.5–12.5 Hz) would actually fall in the range of the lower alpha band of that subject. It is therefore of crucial importance to adjust frequency bands individually for each subject, by using IAF as the cut off point between the lower and upper alpha band (see text).

hippocampus of lower mammals. Its frequency ranges from about 3 to 12 Hz (e.g., Ref. [95]) and, thus, shows a much wider frequency range than in humans where theta lies between about 4 to 7.5 Hz. Its wide frequency range and large power make it easy to observe frequency and power changes in animals. This is in sharp contrast to the human scalp EEG, where—without the help of sophisticated methods—changes in theta frequency are very difficult or almost impossible to detect. The question, thus, is whether there is a physiological criterion that allows us to decide which frequency marks the transition between alpha and theta oscillations.

Alpha and theta respond in different and opposite ways. The crucial finding is that with increasing task demands theta synchronizes, whereas alpha desynchronizes (cf. the bold in relation to dotted line in Fig. 1A). This fact is documented in reviews on event-related desynchronization (ERD) [122,67,68], as well as by a variety of studies using other experimental approaches (e.g., Ref. [45,46,95,99,131,133,129]). If EEG power in a resting condition is compared with a test condition, alpha power decreases (desynchronizes) and theta power increases (synchronizes). Classical findings demonstrate that the decrease in alpha power (suppression of the alpha rhythm) can be observed primarily when subjects close their eyes. More recent evidence, however, suggests that attentional and semantic memory demands are powerful factors which lead to a selective suppression of alpha in different ‘subbands’ and that the well described effects of visual stimulation (e.g., eyes open vs. closed) represent just a special class of sensory-semantic task demands (see Section 4 and Refs. [72,75,78–81]). As already emphasized, encoding of sensory information always aims to extract the meaning of the perceived information which is stored in semantic LTM. Thus, there is a close relation between sensory and semantic encoding.

As Fig. 1 illustrates, that frequency in the power spectra which marks the transition from theta synchronization to alpha desynchronization may be considered the individual transition frequency (TF) between the alpha and theta band for each subject. When using this method to estimate TF, we have found that TF shows a large interindividual variability (ranging from about 4 to 7 Hz) which is significantly correlated with alpha peak frequency [76]. Preliminary evidence for a covariation between theta and alpha frequency was already found by Klimesch et al. [75] and is further documented by Doppelmayr et al. [34]. These findings indicate that theta frequency (as measured by TF) varies as a function of alpha frequency and suggest to use alpha frequency as a common reference point for adjusting different frequency bands not only for the alpha, but theta range as well. For estimating theta power, the individual determination of frequency bands may even be more important because otherwise the effects of theta synchronization are masked by alpha desynchronization particularly in the range of TF (cf. Fig. 1B,C).

1.3. Definition of frequency bands

Because alpha frequency varies to a large extent as a function of age, neurological diseases, memory performance (see Section 2.1 below), brain volume [115,114] and task demands [73], the use of fixed frequency bands does not seem justified. As an example, an elderly subject with bad memory performance may show a peak frequency of 7 Hz or lower [16]. When strictly applying the rule that alpha peak frequency is that spectral component within $f1 = 7.5$ and $f2 = 12.5$ Hz which shows maximal power, we would arrive at the conclusion that the obtained frequency indicates theta instead of alpha frequency. Fortunately, as discussed in the previous section, there is a physiological criterion which allows us to answer this question. If EEG power around 7 Hz would desynchronize during a test—as compared to a resting condition (cf. Fig. 1A)—we still would accept that a peak frequency of 7 Hz indicates alpha but not theta frequency.

This example documents the necessity to define the alpha band individually for each subject as that range ($f1$ to $f2$) ‘around’ the individual dominant EEG frequency (above the lower delta range) that desynchronizes during task demands. In order to avoid confusions with traditional measures, we use the term individual alpha frequency (IAF) to denote the individual dominant (peak or gravity) EEG frequency (in the range of $f1$ to $f2$) of a single subject. The crucial point, of course, is the exact location and individual definition of the frequency limits $f1$ and $f2$. For $f1$, TF is a good estimate, but for $f2$ an obvious physiological criterion is lacking. An indirect way to solve this problem is to define the frequency limits of the lower alpha band by $f1$ and IAF and to assign the ‘remaining’ part of the alpha frequency range (which equals [alpha frequency window] – [IAF – $f1$]) to the upper band. Results from our laboratory indicate that the lower alpha band has a width of about 3.5–4 Hz. Accordingly, the upper alpha band (the frequency range above IAF) is a rather narrow band of 1 or 1.5 Hz, if it is assumed that the alpha frequency window has a width of about 5 Hz. Experimental findings (discussed in detail in Section 4 below) indicate that the upper alpha band—defined as a band of 2 Hz above IAF—responds selectively to semantic LTM demands and behaves in a completely different and sometimes opposite way as the lower alpha band (see also the review in Ref. [121]). Furthermore and most importantly, it was found that the lower alpha band (a band of 4 Hz below IAF) reflects different types of attentional demands. Thus, it was broken down into two subbands of 2 Hz each which are termed lower-1 and lower-2 alpha (see Fig. 1 and Section 4).

In summarizing, when using IAF as an anchor point, it proved useful to distinguish three alpha bands (with a width of 2 Hz each), two lower alpha bands (below IAF) and one upper alpha band (above IAF). The theta band is defined as the frequency band of 2 Hz which falls below

TF. As for the upper frequency limit of the upper alpha band, there are no clear criteria for the lower frequency limit of the theta band. In any case, however, it is important to emphasize that the use of narrow frequency bands reduces the danger that frequency specific effects go undetected or cancel each other. Thus, broad band analyses must be interpreted with great caution. The implication is that an unbiased estimate of alpha and theta power can be obtained only, if the traditional fixed band analyses are abandoned and if narrow frequency bands are adjusted to the individual alpha frequency of each subject. However, the vast majority of studies use broad, instead of narrow alpha bands (cf. Table 1) which in addition are not adjusted individually.

The suggested definition of frequency bands is based on physiological criteria (such as TF and IAF) and on the functional significance of narrow frequency bands (see Section 4). An alternative way to define EEG frequency bands is to analyze the covariance of spectral estimates by multivariate statistical methods such as factor analysis. The crucial question here is whether the activities in different frequency bands vary independently. With respect to the traditional theta and alpha frequency range, results from

factor analyses show at least three independent factors, one for theta, one for the lower alpha band and another for the upper alpha band (see e.g., Ref. [106] and the summary in Ref. [96]). However, the frequency limits vary considerably between studies. As an example, Wieneke (reported in Ref. [96]) found a factor covering the frequency range of 6–9 Hz, which was termed ‘theta’ whereas within that same frequency range, Mecklinger et al. [106] extracted one component which they classified as ‘lower alpha’. Divergent results from factor analyses are due to the type of power measurements (spectral estimates may be expressed in terms of relative or absolute power), type of derivation (e.g., monopolar [referential], bipolar, Laplacian), electrode location, task type (resting condition with eyes open or closed or performance of some task), the selected sample of subjects, and finally the method used to extract and rotate factors. It also should be emphasized that factor analyses are usually performed on the basis of a correlation matrix which was obtained by correlating spectral estimates over a sample of n subjects. Done in this way, the extracted factors represent average frequency ranges of that particular sample. However, factor analysis could also be used for an individual definition of fre-

Table 1
EEG alpha activity: frequency limits and peak (#) or gravity (*) frequency

Ref. no./author	Broad band	Subbands	Der.	N	Age	α -frequency
[1] Alloway et al.	8–12	–	M	10	29–62	–
[2] Anokhin and Vogel	8–13	–	M	101	20–45	–
[11] Besthorn et al.	–	7.5–9.5; 9.5–12.5	M	92	59–78	–
[14] Boiten et al.	8–13	–	M	8	22–29	–
[16] Brenner et al.	–	8.0–9.9; 10–12.9		119	51–89	6–14,r
[17] Breslau et al.	8.2–12.9	–	M	33	18–78	–
[24] Chiaramonti et al.	8–11.5	–	M	55	51–81	–
[27] Coben et al.	8–13	–	B	127	64–83	6.9–9.3*
[36] Duffy et al.	8–11.75	–	M	63	30–80	7.5–13#,r
[44] Gevins et al.	8–13	–	M	55	–	–
[55] Hartikainen et al.	7.6–13.9	–	B	52	33–78	9.6–10.1#
[61] Jausovec	7.5–13	–	M	60	18–19	–
[62] John et al.	7.5–12.5	–	B	648	1–21	–
[65] Kaufman et al.	8–12	–	MEG	3	–	–
[87] Könönen and Partanen	7.6–13.9	–	B	54	23–80	–
[89] Krause et al.	–	8–10; 10–12	M	10	23–41	–
[99] Marciani et al.	8–12.5	–	C	60	19–89	–
[117] Obrist et al.	–	–		57	65–84	7.5–9.2#
[124] Pfurtscheller	–	1 or 2 Hz bands	M, B	§	§	–
[132] Salenius et al.	7–14 Hz	–	MEG	13	20–49	9.3–11#,r
[134] Schmid et al.	7.4–12.5	–	B	536	5–11	–
[139] Somsen et al.	7.5–12.5	–	M	142	5–12	4.5–10#
[146] Sterman et al.	–	2 Hz bands 5–15	M	26	25–39	–
[153] Szeliés et al.	8–13	–	M	58	53–78	–
[156] Torres et al.	–	–	M	182	48–88	9.4\$,S.D. = 1
[157] Torsvall and Akerstedt	8–11.9	–	B	11	27–58	–
[162] Wada et al.	7.5–12.5	–	M	264	3–26	–
[164] Wieneke et al.	–	3 db below peak	M	110	18–50	9.9#,S.D. = 1
[166] Williamson et al.	8–13	–	MEG	§	§	–

Der. = Derivation; M = monopolar; B = bipolar; C = Common average reference; N = sample size; §, Reviewed data; r, range for lowest and highest frequency; \$, Dominant frequency, defined by period of alpha wave.

quency bands, if the EEG of a single subjects is used and if spectral estimates are correlated over a series of n trials (epochs).

Even if frequency bands are defined individually for each subject, it must be emphasized that EEG frequencies vary between recording sites. As an example, it is well known that alpha waves occur primarily during wakefulness over the posterior regions of the head and can be best seen with eyes closed and under conditions of physical relaxation and mental inactivity [110]. The frequency of alpha waves is faster at posterior and slower at anterior recording sites. It would, thus, be desirable to adjust frequency bands not only individually for each subject but also for each recording site. For practical reasons, this has not yet been done.

1.4. Oscillatory components in the EEG

In an empirical sense, an oscillatory component is defined by the presence of a rhythmic activity in the EEG which is manifested by a ‘peak’ in spectral analysis. In contrast to theta, alpha as the dominant rhythmic activity, characterized by sinusoidal wave forms, clearly meets this definition. In the human EEG of young healthy adults, there are at least two other oscillatory components, the mu rhythm and the third rhythm. The mu rhythm (mu stands for motor) has an arch-shaped wave morphology, appears over the motor area and becomes suppressed (desynchronized) during motor related task demands (see the extensive work of Pfurtscheller et al., e.g., Ref. [125]). Other terms are ‘arcade’, ‘comb’ or ‘wicket’ rhythm, ‘central’, ‘rolandic’ and ‘somatosensory’ alpha (cf. the review in Ref. [110] p. 137f). The third rhythm which is not detectable in the scalp EEG (but e.g., by the use of epidural electrodes or magnetoencephalography [MEG]) is independent from the (posterior) alpha and mu rhythm and appears over the midtemporal region [110]. In emphasizing the fact that (in the MEG) this rhythm is best seen over the auditory cortex in the temporal lobe, Hari [51] uses the term ‘tau’ rhythm (tau stands for temporal). There is some evidence that the tau rhythm becomes suppressed during acoustic but not visual stimulation (cf. the review in Hari et al. [52]). Because the focus of this review is on theta and alpha activity with respect to cognitive performance and memory, the mu and third rhythm will not be considered.

Despite the fact that theta does not meet the criteria for an oscillatory component in the EEG, it may still be argued that activity within the individually defined theta band reflects oscillatory processes. In a theoretical sense, the EEG can be conceived of a linear superposition of a set of different sine waves (oscillatory components). In addition, there are more specific arguments which are based on empirical evidence:

1. With the help of sophisticated methods, theta peaks can be found in the human scalp EEG of young healthy adults [45].

Table 2

Double dissociation between tonic and phasic (event-related) changes in alpha and theta power with respect to cognitive performance

	Increasing performance		Decreasing performance	
	Theta power	Alpha power	Theta power	Alpha power
Tonic change	Decreases	Increases	Increases	Decreases
Phasic change	Increases	Decreases	Decreases	Increases

Tonic changes are discussed in Section 2, phasic changes in Section 4 below.

A phasic change is measured as an increase or decrease in band power during task performance as compared to a reference or resting period (cf. Fig. 7).

2. Theta frequency (as measured by TF) covaries with alpha frequency (as measured by IAF [34,76]).
3. Theta and alpha band power are related to each other, although in a reciprocal or ‘opposite’ way (see Sections 2–4 below and Table 2),
4. Animal research has shown that theta clearly is an oscillatory component of the hippocampal EEG which is related to memory processes (see e.g., the review by Miller [107] and Section 5 below),
5. Research from our laboratory indicates that theta band power increases in response to memory demands just as hippocampal theta in animals does (see Sections 4.3 and 5 below).

Thus, the concepts of desynchronization and synchronization will also be used for the (individually defined) theta band. In a similar way, these concepts will be applied to the different subbands of alpha. Visual inspection of ‘alpha waves’ in the EEG may invite the misleading interpretation that there is only a single rhythm which may just vary in frequency. As the results from factor analyses have shown, there are at least two independent components of alpha activity which must be distinguished. Based on physiological and experimental evidence, many authors meanwhile assume that there is an entire population of different alpha rhythms (e.g., Refs. [6,166,167]). Thus, it seems quite obvious to assume that during desynchronization different alpha rhythms in different subbands start to oscillate with different frequencies (for more details see Section 5).

2. Tonic changes and differences in the alpha and theta frequency range

The type of EEG changes or differences which are discussed in the following sections may be termed ‘tonic’ in order to contrast them from ‘phasic’ changes. Phasic (or event-related) changes in the EEG are more or less 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. Phasic changes in the EEG are task and/or stimulus related. Tonic changes, on the other hand,

occur over the life cycle and in response to circadian rhythms, fatigue, distress, neurological disorders, etc.

2.1. Age related changes and performance related differences in alpha frequency

It is a well documented fact that alpha frequency changes with age. From early childhood up to puberty alpha frequency increases, but then starts to decline with age. For children, Hughes [60] reports that alpha frequency for 1, 3, 9 and 15-year olds increases from about 5.5 to 8, 9 and 10 Hz, respectively. Similar estimates were reported by Somsen et al. [139] and Niedermeyer [112]. It should be noted, however, that the increase in alpha frequency and changes in alpha power are not linear, but occur in several growth spurts [38,59,155]. Within the age range of adult subjects Köpruner et al. [88] have found a linear relationship (alpha peak frequency = $11.95 - 0.053 \times \text{age}$) between age and alpha frequency. 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. It is important to note that even in a sample of age-matched subjects, interindividual differences are about as large as age-related differences. When interindividual variability is described

in terms of a normal distribution [67], about a third of young adults are expected to show a difference in alpha frequency of more than 2 Hz.

With respect to an age related decrease in alpha frequency there is some discussion about its general validity. As an example, Duffy et al. [36] report only a slight and non-significant drop in alpha peak frequency. Closer inspection of their results, however, reveal that their finding is due to a lack of decrease in alpha frequency during the early and middle adult age range (from about 30 to 50 years). For older subjects, a drop of about 1 Hz was found between 60 and 80 year olds. Other studies have found evidence that an age related decrease in alpha frequency may not be due to age per se but instead to age related neurological diseases [58,156] or to a lack of school education (cf. Ref. [53]). Nonetheless, changes in alpha frequency as schematically depicted in Fig. 2 give a good overall picture of the respective results reported in the literature.

The findings of several experiments suggest that alpha frequency is an indicator for the speed of cognitive and memory performance in particular. Early findings reported by Surwillo [147–152] indicate that alpha frequency is significantly correlated with the speed of information processing as measured by reaction times (RT). Subjects with

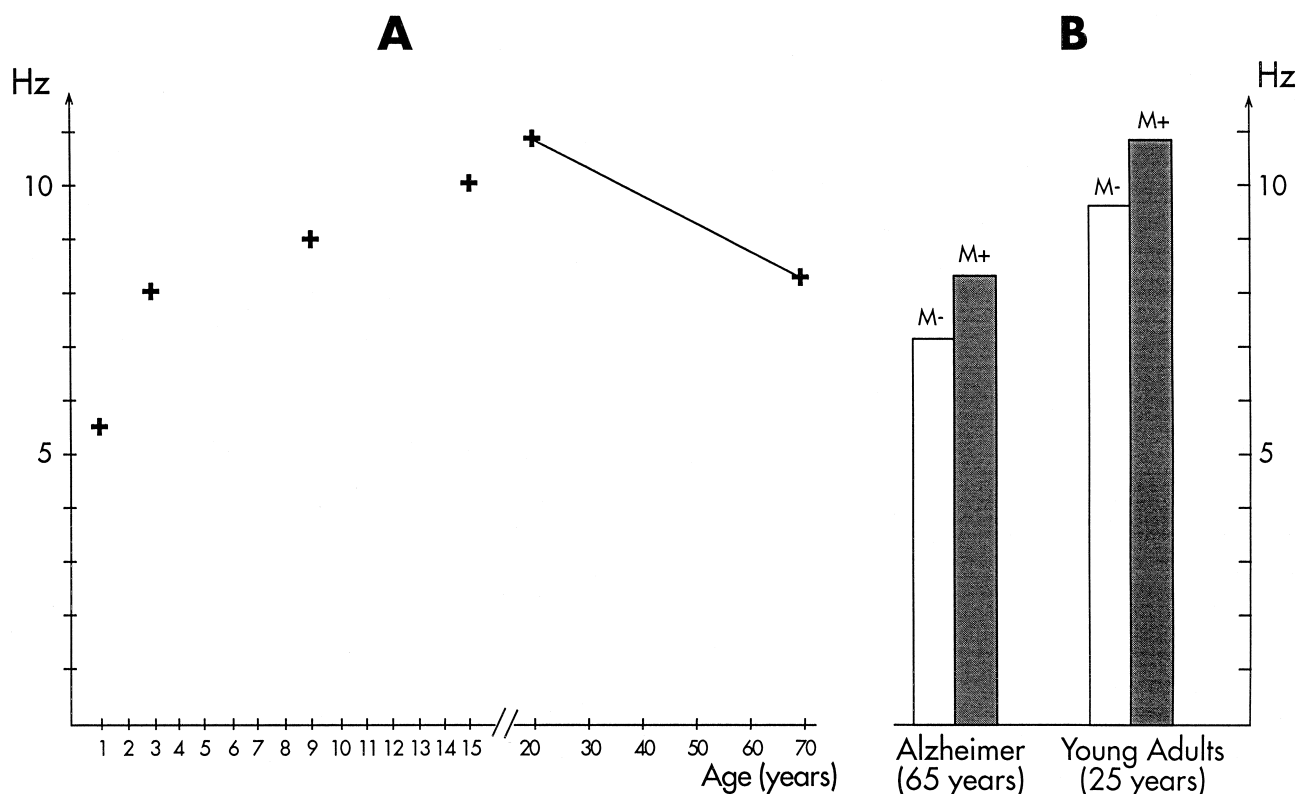


Fig. 2. Interindividual differences in alpha frequency are large and vary with age and memory performance. (A) From early childhood to puberty, alpha frequency increases from about 5.5 to more than 10 Hz but then starts to decrease with age. This decrease in alpha frequency may be due to age related neurological diseases or even to the lack of 'mental training' in the later lifespan but not to age per se. (B) As compared to bad memory performers, good performers have a significantly higher alpha frequency. This holds true not only for young and healthy subjects (e.g. Refs. [69,71,73] but even for Alzheimer demented subjects [71].

high alpha frequency show fast RTs, whereas slow subjects have low alpha frequency (for similar results see also Ref. [77]). These findings are in good agreement with the results from a variety of experiments from our laboratory which revealed that alpha frequency of good memory performers is about 1 Hz higher than that of age-matched samples of bad performers [67,68,70,71,73,74]. Because good performers are faster in retrieving information from memory [66] than bad performers, these data too indicate that alpha frequency is related to the speed of information processing or reaction time. These results also suggest that alpha frequency should be related to intelligence which indeed seems to be the case ([2]). All of these findings are based on interindividual differences in alpha frequency. In contrast, intraindividual or task related shifts in alpha frequency appear not to be related to the speed of information processing [76] because an asymmetric desynchronization in the broad alpha band (favoring the lower or upper band) will lead to a shift in power and, thus, to a distorted estimate of alpha frequency.

In summarizing, the reported findings suggest that alpha frequency is an indicator of cognitive and memory performance. This conclusion is also supported by the fact that alpha frequency increases from early childhood to adulthood and then decreases with age over the remaining life span in a similar way as brain volume and general cognitive performance does (e.g., Refs. [12,165]).

2.2. Age related changes in alpha and theta power

The extent of age related frequency and power changes in children are depicted in Fig. 3A (data are from Somsen et al. [139]). At an age of 12 years (dashed line) children show already a well developed alpha peak at about 10 Hz. In contrast, for 7-year old children, two different peaks, a theta peak (centered at 4.5 Hz) and an alpha peak (located at about 9 Hz) can be observed. As compared to younger children, 12-year olds exhibit a strong decrease in theta power and a pronounced increase in upper alpha power.

When broad band differences within the traditional frequency ranges (cf. the vertical lines in Fig. 1) are calculated, the age related increase in absolute alpha power is blurred. The reason for this is that due to an increase in alpha frequency, peak alpha power shifts towards higher frequencies. As a consequence, the upper alpha band shows an increase in power whereas the opposite holds true for the lower alpha band (cf. Fig. 3A). Thus, for the broad alpha frequency range, little or no age related differences are obtained. Misleading interpretations that arise from this fact can easily be demonstrated by considering the results of a broad band analysis as depicted in Fig. 4 (data are again from Somsen et al. [139]). Age related changes in broad band absolute power (delta: 1.5–3.5 Hz, theta: 3.5–7.5 Hz, alpha: 7.5–12.5 Hz, beta: 12.5–22.5 Hz) indicate large differences in the delta and theta but no changes (or

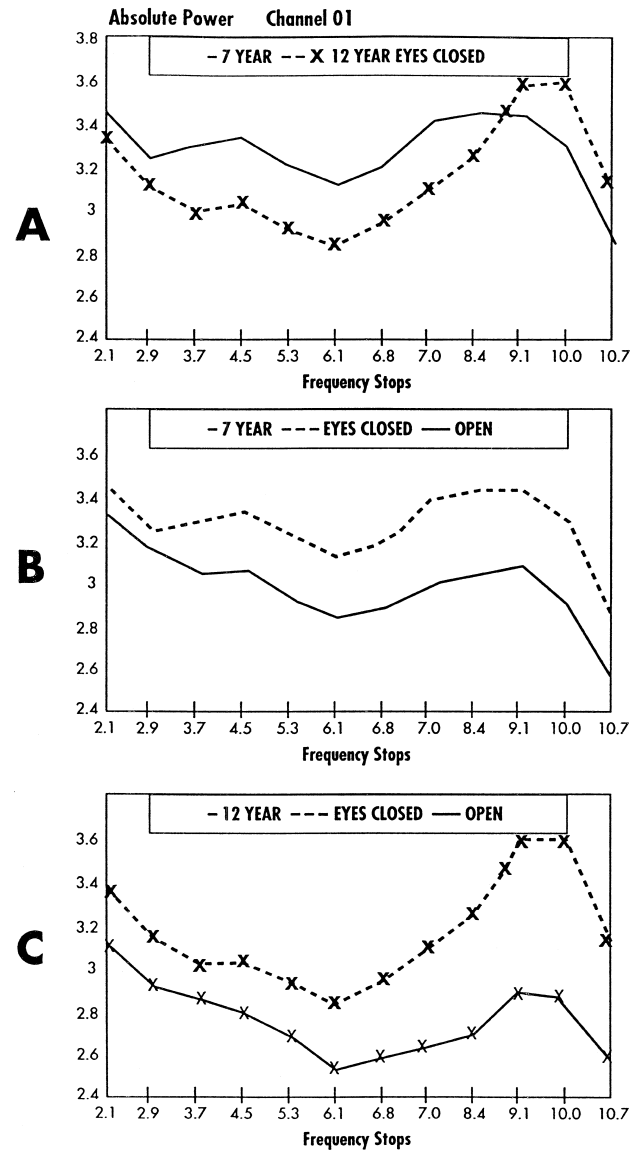


Fig. 3. Power spectra for 7 and 12 year old children (data replotted from Ref. [139], p. 201; reprinted with permission). (A) As compared to young children, older children show a pronounced increase in upper alpha power and a strong decrease in theta and delta power. Power suppression during eyes opening is smaller for young (B) as compared to older children (C).

even a slight decrease) in the alpha band (cf. the left part of Fig. 4). If relative, instead of absolute power is calculated, a different pattern of results emerges as the diagrams in the right part of Fig. 4 indicate. Here, in agreement with the data of Fig. 3, delta and theta power decreases, whereas alpha power increases. The reason for this difference between absolute and relative power can easily be explained when considering the fact that relative power measurements tend to give larger estimates for the dominant frequency range (where absolute power is largest) and lower estimates for frequencies which fall outside this range. As a consequence, when alpha becomes the dominant frequency with increasing age, relative power measurements will show a pronounced age related increase in

Absolute Power

Relative Power

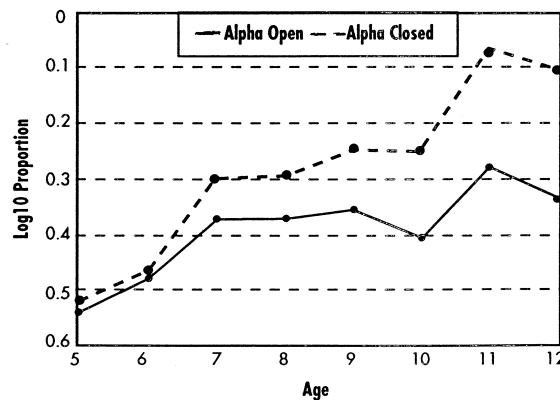
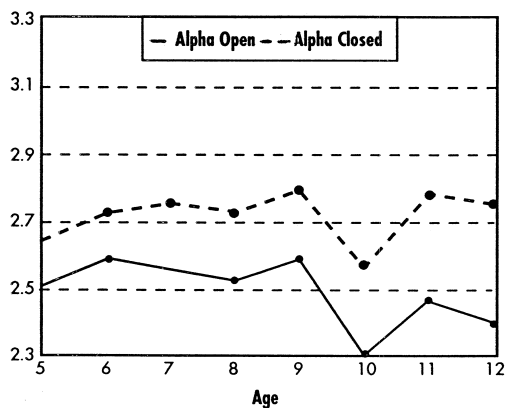
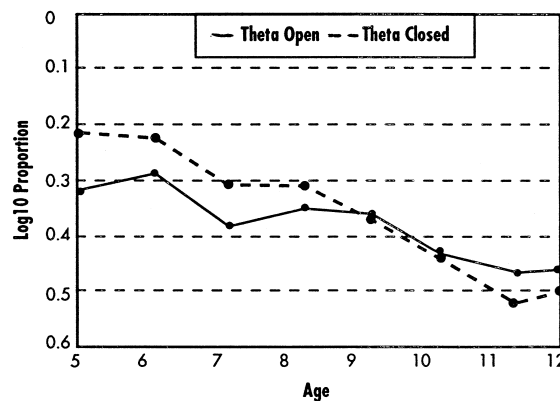
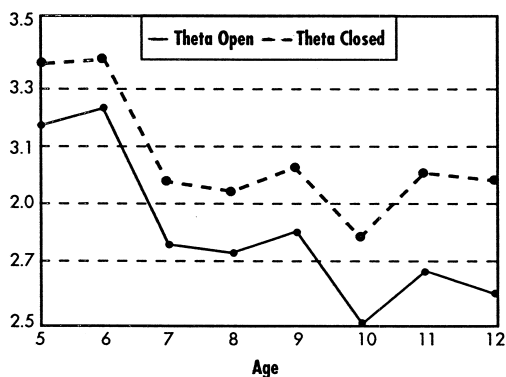
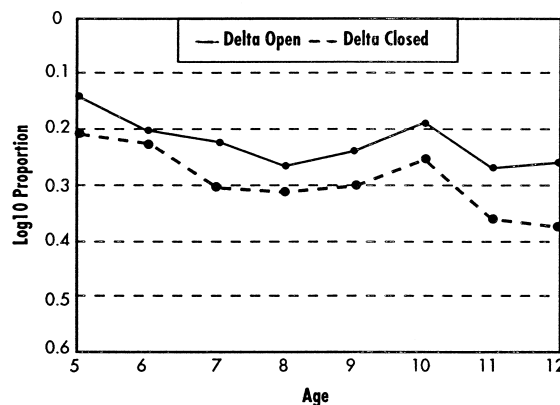
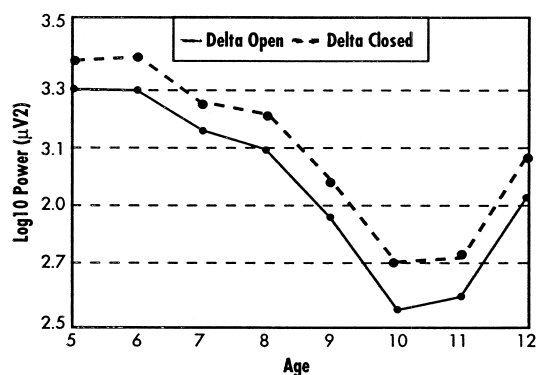


Fig. 4. Differences between age related changes in absolute and relative power (broad band analysis; data replotted from Ref. [139], pp 194–195; reprinted with permission). Because individual alpha frequency changes with age (cf. Fig. 2) and because broad band analyses use fixed frequency windows, the strong age related increase in upper alpha power is blurred (cf. Fig. 1). Relative power measures give better estimates for the alpha band because (i) they yield larger measures for the dominant frequency range and because (ii) with increasing age, alpha power becomes the dominant frequency in the EEG.

alpha power. This divergence in age related changes in absolute broad band and relative alpha power were obtained by many other studies (e.g., Ref. [54]).

The findings reported by Somsen et al. [139] are in good agreement with earlier studies. It has been shown repeatedly that absolute power in the delta and theta band

decrease with age while relative alpha power (or absolute upper alpha power) increases [42,53,54,62,63,105]. Studies investigating developmental changes in topography have found that the increase in alpha power starts at posterior derivations and ends at more anterior recording sites ([43], for similar results see also Ref. [162]). The increase in

alpha power is even more remarkable, if one considers findings reported by Yordanova and Kolev [169] which indicate that phase locking in the alpha frequency range also increases with age.

The conclusion from the studies reviewed so far is that the mature brain at or beyond an age of about 16 is characterized by an increase in absolute power in the upper alpha band but by a decrease in theta and delta power as compared to a less developed brain in younger children. A series of other studies support this view and show further that children with poor education [53], with reading writing/disabilities [54], with spelling disabilities [21] or with other types of neurological disorders [134] show significantly more delta and theta but less alpha power (for a review see also Ref. [134]).

For older subjects (about 50 years and older) a variety of studies have found age related changes in EEG power (e.g., Refs. [26,103,116,164] and the reviews in Refs. [110–112,160]). Most of these studies show a general slowing of the EEG with a pronounced power increase in the slow frequency ranges of about 7 Hz and below and a decrease in higher frequencies of about 7 Hz and higher (e.g., Refs. [26,101,116,117]).

A very similar pattern of results is obtained for cognitively impaired or demented subjects. As compared to age matched controls, the EEG of demented subjects is characterized by an increase in theta, a decrease in alpha power and alpha blocking and a forward shift in alpha activity from posterior to more anterior recording sites (e.g., Refs. [11,24,27,64] p. 995, [138,153]). It should be noted, however, that a few studies report that demented [16] or old subjects [87] show even an increase in alpha power. In the study of Brenner et al. [16] this effect was restricted to the lower alpha band. Könönen and Partanen [87] used a bipolar montage and, thus, their findings reflect effects that are topographically restricted and may, thus, not be related to changes in absolute or relative power as reported in other studies (cf. the overview in Table 1).

Reports on age related changes in alpha and theta power must be interpreted with caution because most of the studies used broad band analyses within fixed frequency windows. In older subjects at an age of about 60–70 years alpha frequency lies between 8.5 to 9 Hz. As a consequence, the traditional alpha range of 7.5–12.5 Hz will miss most of the ‘real alpha range’ (cf. Fig. 1B,C) and will instead reflect only a small part of the ‘real’ upper alpha band. On the other hand, the traditional theta band of 4–7.5 Hz will reflect most of the slowed alpha activity. Thus, an age related decrease in alpha may be masked by an age related increase in theta. Depending on the age of the subjects and their averaged alpha frequency, some studies report either a lack of an age related change in the alpha band (e.g., Ref. [99]) or even an increase (e.g., Ref. [16]) which might actually be due to an increase in theta.

In summarizing, the reported findings suggest that alpha (particularly in the range of the upper alpha band) and

theta change with age in a nonlinear and opposite way. There is a strong increase in alpha but decrease in theta and delta from early childhood to adulthood. During adulthood alpha and theta power may remain comparatively stable but at least beyond the age of 50 or 60 years [17] a period of a pronounced decrease in alpha and increase in theta power can be observed which may well be due to age related neurological disorders and not to age per se [58,55]. It is interesting to note that sedative drugs (benzodiazepines or barbiturates) which are known to cause different degrees of amnesia have the common effect of suppressing the alpha rhythm [40].

2.3. Age related changes in alpha and theta reactivity

Measures of alpha or theta reactivity usually reflect power differences between two resting periods, one with eyes open, the other with eyes closed. The term alpha reactivity or suppression also is used when a resting period (eyes open or closed) is compared with a test period in which subjects have to perform some type of task. It is well known since Berger (e.g., Ref. [10]) that opening eyes and mental activity suppresses the alpha rhythm.

For children several studies have found an age related increase in alpha reactivity (e.g., Ref. [139]). Inspection of Fig. 3B,C demonstrates a strong age related increase in alpha reactivity with increasing age. However, it should also be noted that even in the delta and theta band a pronounced suppression of power can be observed (Fig. 4). This is in sharp contrast to respective findings with adults where the effects of power suppression are restricted to the alpha band. It remains an open question why power suppression during eyes open in children affects even the delta and theta band. It may be hypothesized that in children different frequency bands are not yet functionally differentiated and separated from the broad alpha frequency range and, thus respond more in an alpha-like way.

Within the age range of older subjects, it is well known that alpha reactivity or suppression tends to decrease with age (e.g., Ref. [36]). Similar effects were found when neurologically impaired subjects were compared with age matched controls (e.g., Ref. [1,11]). As an example, Sheridan et al. [136] have reported that Alzheimer demented subjects with normal alpha that is suppressed during eye opening have significantly higher WAIS Performance IQ scores than patients with irregular alpha that does not or only weakly change during eye opening. Similar findings were obtained even with learning disabled children (c.f., Ref. [41]) who show less task-related alpha attenuation than age-matched controls.

2.4. Changes in alpha and theta power during the wake-sleep cycle

The evidence reviewed so far suggests that comparatively large alpha but small theta and delta power characterize the EEG of subjects with good cognitive perfor-

mance. Thus, it appears plausible to assume that during the transition from alert wakefulness to sleep onset alpha power decreases whereas theta and delta power increase. This is indeed the case as is known since the pioneering work by Dement and Kleitman [32]. More recent studies distinguish between 9 different EEG stages within the hypnagogic state (i.e., the transition period from waking to sleeping) as is shown in Fig. 5.

By using spectral analysis and comparatively narrow bands in the extended alpha frequency range (alpha 1: 7.6–9.4 Hz; alpha 2: 9.6–11.4 Hz; alpha 3: 11.6–13.4 Hz), Tanaka et al. [154] found that absolute delta and theta power increase, whereas alpha 1 and alpha 2 decrease from EEG stage 1 to 7 (see also Ref. [56]). Power in the alpha 3 band, which already reflects parts of slow sigma activity (sigma is the frequency range of about 12.5–15 Hz where sleep spindles occur) decreases from EEG stage 1 to 6 but increases from 6 to 9. Furthermore, from stage 1 to 9, the topographical region of maximal alpha power (in all of the three bands) moved from posterior to anterior recording sites, as Fig. 6 indicates. This is reminiscent of ‘alpha anteriorization’ which was found for demented subjects (e.g., Ref. [24]). It is also interesting to note that the largest drop in alpha power was found in the alpha 2 band which corresponds to the traditional upper alpha band (when considering the mean age of subjects which was 23 years).

Sleep spindles (starting at EEG stage 8, cf. Fig. 5) usually are taken as sign for the onset of sleep. However,

sleep spindles appear rather gradually and, thus, the precise time of actual sleep onset is difficult to determine. This question was addressed in an interesting study by Ogilvie et al. [118]. Before the sleep session began, subjects were instructed to press a button if a tone was presented. As was expected, with increasing drowsiness the reaction time for pressing the button increased. During that period of increasing drowsiness (but when subjects were still responding to the tone) delta and theta power increased, whereas alpha decreased. However, when responding ceased, EEG power increased across all frequency bands. A comparison with the data of Tanaka et al. [154] suggests that actual sleep onset occurs already during EEG stage 6 and 7, much earlier than the first spindles appear. It is important to note, however, that during sleep onset alpha power shows about the same magnitude as compared to a state of very low drowsiness when subjects gave a fast response to the tone. As compared to this stage, the increase in power during actual sleep onset (measured as a percentage of increase in absolute power) for delta, theta, alpha (8–12 Hz), sigma and beta (15–25 Hz) is 56%, 211%, 3%, 177% and 56%, respectively. Thus, the abrupt increase in EEG synchronization during sleep onset occurs in a broad frequency range that only marginally affects the alpha band. As the data in Fig. 6 demonstrate, during sleep onset (at about EEG stage 6 and 7) alpha power (in the range of 7.6–11.4 Hz) is still much smaller than during alert wakefulness (EEG stage 1).

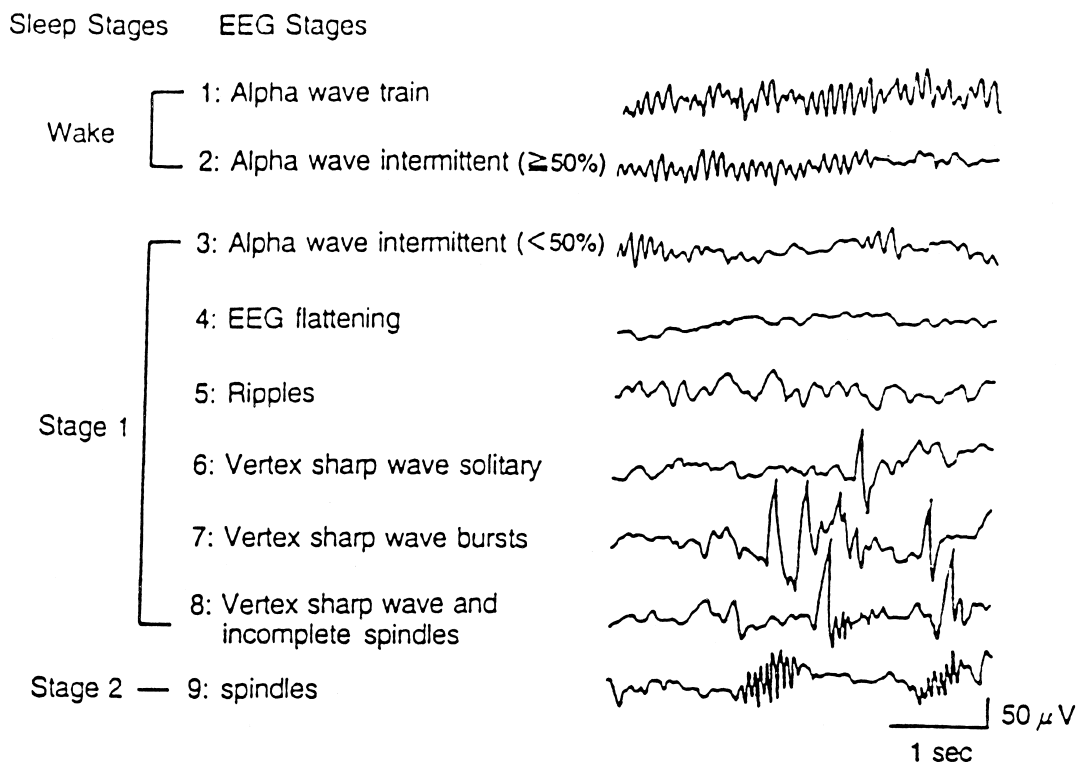


Fig. 5. Typical EEG patterns during the hypnagogic state which is the transition period from waking to sleeping (reprinted from Tanaka et al., Ref. [154], p. 524; reprinted with permission from the American Sleep Disorders Association and the Sleep Research Society, Rochester, MN (1997)). Even visual inspection of the EEG indicates that alpha activity decreases during the early EEG stages 1–4.

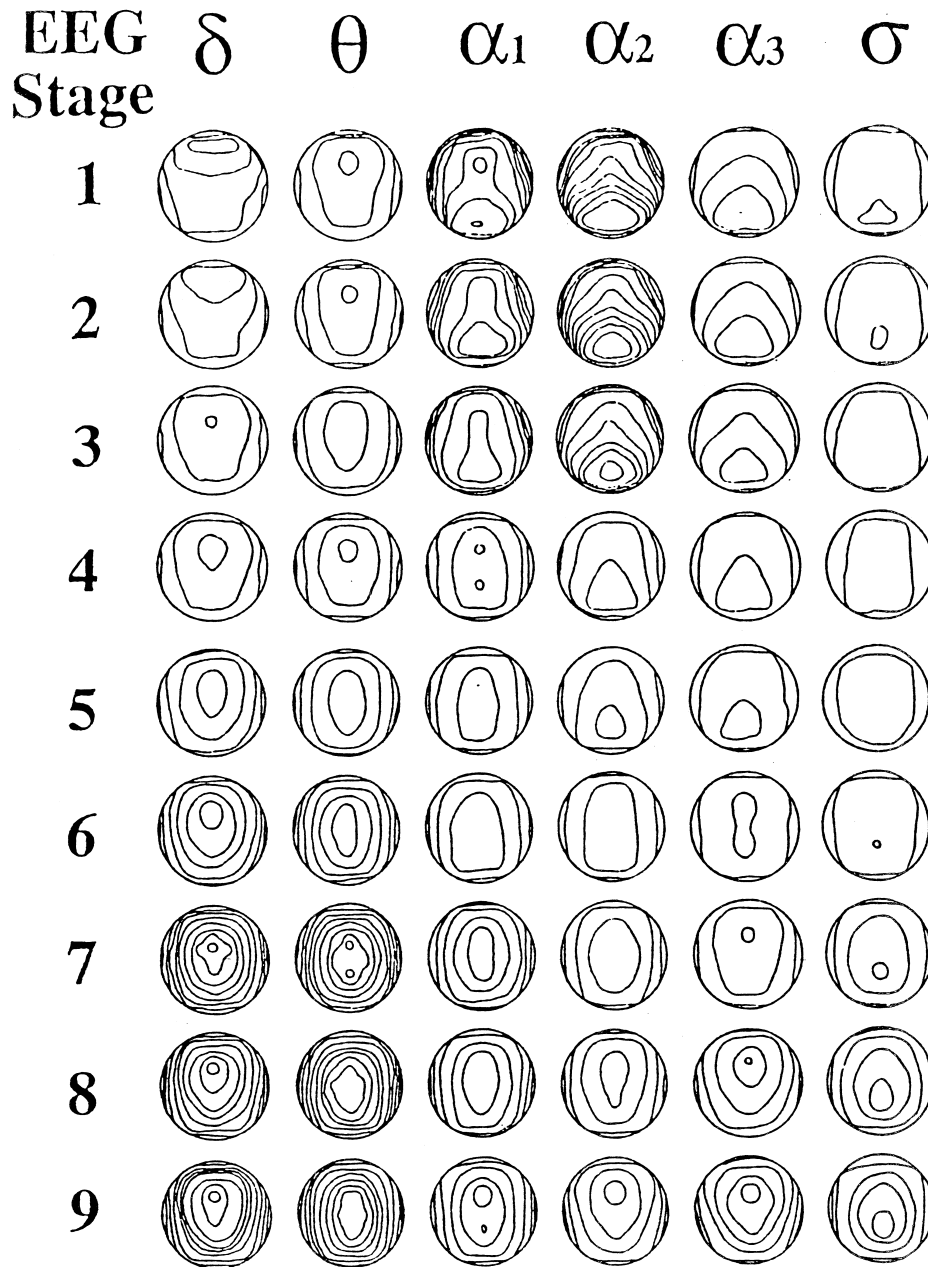


Fig. 6. Average topographic maps for six frequency bands, showing changes in absolute power during the 9 EEG stages in the hypnagogic state (reprinted from Tanaka et al., Ref. [154], p. 527; reprinted with permission from the American Sleep Disorders Association and the Sleep Research Society, Rochester, MN (1997)). As discussed in the text, actual sleep onset occurs during EEG stage 6 or 7, much earlier than the first spindles appear (cf. Fig. 5). Up to these stages alpha power (in all of the three bands) shows a strong decrease, whereas the opposite holds true for the theta and delta band. Furthermore, alpha power moves from posterior to anterior recording sites. This is reminiscent of 'alpha anteriorization' which was found for demented subjects.

REM sleep is characterized by a low voltage desynchronized EEG with an irregular pattern of bursts or trains of alpha activity particularly at occipital leads [32,145]. As compared to EEG stage 1 and 2 (cf. Fig. 5) alpha activity generally is decreased during REM sleep [50]. Because of this fact and the high probability of dreaming episodes during REM, it appears likely that the decrease in alpha during parts of the REM sleep can be interpreted in terms of an 'event-related' suppression or 'desynchronization' of

the kind that can be observed during an alert subject performing some type of task (for more details see Section 4 below). Evidence for this assumption comes from an interesting study by Chong-Hwa Hong et al. [25]. In a single subject design, 12 different dreams during REM sleep were analysed. After a dream, the subject was awakened and had to report the dream which was scored for 'language content'. The results showed that the higher the score for expressive or receptive language was, the larger

was the suppression of alpha power at those recording sites that correspond to Broca's and Wernicke's area.

During eye movements (EM's), regardless of occurring during REM or NREM sleep, alpha increases but theta decreases [27] (see also Ref. [50]). It is known that PGO spikes are highly correlated with dream activity and precede (or may even trigger) EM's. In a study conducted by Conduit et al. [28] the appearance of EM's in stage 2 sleep was used to provoke dream episodes. Their basic idea was that EM's indicate PGO spikes and to present during that period light and sound stimuli (below waking threshold) in order to provoke a dreaming episode. The results show that in the experimental condition (as compared to control conditions with EM's but no stimulation) a significant increase in alpha power and a higher frequency of imagery reports was obtained after awakening. These data suggest that the increase in alpha activity reflects some sort of visual arousal that precedes a dream with high imagery content.

The effects of sustained wakefulness and sleep deprivation on EEG power are well documented (e.g., Refs. [15,29,31,33]) and in general show that increased theta and lower alpha power reflect increased sleepiness. As an example, Cajochen et al. [22] have found that absolute EEG power within the range of 6.25–9 Hz increases monotonically during sustained wakefulness in a sample of subjects with a mean age of 53 years. Considering the age related decline in alpha frequency (cf. Ref. [88] and Fig. 2A), the expected alpha frequency for these subjects is about 9 Hz. Thus, the frequency range of 6.25–9 Hz covers the entire range of the (individually adjusted) lower alpha band. Similar findings were obtained by Torsvall and Akerstedt [157]. These results seem to indicate that an increase in lower alpha power may reflect the increased efforts (and probably difficulties) of subjects to maintain a state of alert wakefulness. This interpretation is also supported by Crawford et al. [30] who have found that in contrast to subjects with high sustained attention, low sustained attention subjects which have difficulties to inhibit distracting environmental stimuli show a significantly larger proportion of lower alpha power.

It is interesting to note that an increase in lower alpha power occurs only when subjects are not allowed to fall asleep and when they are forced to stay awake. If tired subjects are allowed to fall asleep, alpha power (including slow alpha frequencies) decreases (cf. Figs. 5 and 6). Thus, during the normal state of increased sleepiness which is correlated with increasing melatonin secretion in the respective circadian phase, we would not expect that (lower) alpha power increases selectively. During a state of decreased mental inactivity such as during increased normal sleepiness, a decrease in alpha and an increase in theta is to be expected. The results reported by Cajochen et al. [23] are in good agreement with this interpretation. These authors have shown that the administration of melatonin leads to a significant increase in absolute power in the

frequency range of 5.25–7 Hz. Considering the mean age of their subjects (which is about 25 years) indicates that the frequency range of significant power differences lies in the theta band (expected alpha frequency is about 10.5 Hz, the lower alpha band ranges from about 7–10.5 Hz). Furthermore, inspection of the time course of power changes between 1700 h and 1900 h reveals a general decrease in alpha power (cf. Ref. [23] p. 210, Fig. 1).

2.5. Alpha power in congenital blindness

Visual information processing represents an important aspect of cognitive performance. If alpha power is indeed positively related to cortical information processing, it would be expected that congenitally blind subjects lack alpha activity at occipital recording sites. This is indeed the case as the following studies indicate. Noebels et al. [113] report that in a sample of 7 congenitally blind adults, the occipital alpha rhythm was absent, whereas slow negative potentials were similar to those of normally sighted controls. Most interestingly, in blind subjects, a pronounced alpha rhythm could be observed at Cz and Fz which was larger in power than that of controls. Thus, it appears as if in more anterior cortical regions a compensatory increase in alpha activity takes place. Similar results were already reported by Birbaumer [13], who found that in congenitally blind subjects alpha activity was reduced occipitally but significantly increased frontally in relation to controls.

3. Interim discussion

If the EEG of the mature brain of young healthy adults is compared either with the developing brain, the aging brain or the brain which is affected by neurological diseases of various kinds, the conclusion is that:

- (a) alpha frequency is positively related to cognitive performance, and
- (b) large power in the range of the upper alpha band but small power in the theta frequency range indicate good cognitive performance.

These conclusions are based on findings which show that

- (a1) alpha frequency increases from early childhood to adulthood but then decreases with increasing age or age related neurological diseases,
- (a2) alpha frequency is lowered in demented subjects (as well as in patients with other types of neurological disorders),
- (a3) alpha frequency is significantly higher in subjects with good memory performance as compared to age matched controls with bad memory performance,
- (a4) alpha frequency is positively correlated with the speed of processing information,
- (b1) theta power decreases and upper alpha power increases from early childhood to adulthood,

- (b2) theta power increases and upper alpha power decreases during the late part of the lifespan,
- (b3) theta power is enhanced and alpha power lowered in subjects with a variety of different neurological disorders as compared to age matched controls (this holds true not only for demented subjects but also for children with reading/writing or spelling difficulties),
- (b4) during the hypnagogic state (i.e., the transition from waking to sleeping) when the ability to respond to external stimuli decreases, theta power increases and upper alpha power decreases.

The behavior of lower alpha shows a somewhat different pattern of results and requires some additional explanation. Old subjects (e.g., Refs. [26,101,116,117]), subjects with difficulties in maintaining a state of alert wakefulness [30] and during a state of sustained wakefulness [22], power in the lower alpha band is increased. Findings from our laboratory [72,73,75,78,83] have shown repeatedly that the lower alpha band responds selectively to attentional demands. A tonic increase of lower alpha power may, thus, reflect the attempt of old or drowsy subjects to increase their attention and alertness. Because the increase in lower alpha power may reflect an attempt to increase cognitive performance (particularly under conditions that are less favourable), large power in the alpha band is again linked to good performance in the sense that if lower alpha power would drop, cognitive performance would drop too.

The conclusions as outlined above holds true only for tonic but not for phasic changes in the EEG. The best known example of a phasic change is the suppression of the alpha rhythm during eyes opening. The results of spectral analyses show that compared to closed eyes, alpha power decreases but theta power increases. As was mentioned in Section 1, this characteristic type of a phasic change in alpha and theta band power can be observed in response to a large variety of different task demands.

At this point we arrive at an interesting paradox. During actual cognitive performance (as compared to a resting state), the EEG is characterized by increased theta but decreased alpha power and thus resembles the EEG during a tonic change that reflects decreased cognitive performance. In Section 4.4 it will be shown that the extent of an event-related change in alpha and theta depends on absolute alpha and theta power. If theta power is low, theta synchronization is large and if alpha power is large, the extent of alpha power desynchronization (suppression) is large too. It is important to note that in a pure statistical sense, the extent of an event-related band power change may very well be independent from absolute power as measured during a resting condition. Thus, the dependency of event-related on absolute power indicates a special physiological mechanism which possibly operates to increase the signal to noise ratio (from a 'reference' to a 'test' interval; cf. Section 4 below).

It will be demonstrated that alpha and theta power on the one hand and event-related changes in alpha and theta

power on the other hand show a double dissociation with cognitive performance: Large alpha power which is correlated with a pronounced decrease in event-related band power and small theta power which is correlated with a pronounced increase in band power indicate good cognitive performance. First positive evidence for the suggested hypothesis comes from age related differences in theta and particularly in alpha reactivity. As mentioned above, from early childhood to adulthood alpha power as well as alpha reactivity (suppression) increases, whereas in older subjects alpha power and alpha reactivity decrease. The complex relationship of this double dissociation is summarized in Table 2.

4. Event-related (phasic) changes in the alpha and theta band

Since the work of Berger it was suggested that visual (or other sensory) task demands and visual attention in particular are the primary factors that lead to a suppression of the alpha rhythm (e.g., Refs. [108,130]). In using event-related desynchronization (ERD), a method introduced originally by Pfurtscheller and Aranibar [123], recent research has revealed a much more complex picture.

A typical example of an EEG epoch which is used for measuring ERD is shown in Fig. 7. The subjects' task was to read a visually presented word and to make a semantic judgment by responding 'yes' to a word denoting a living and 'no' to a word denoting a non-living object. Before a word appeared a warning signal is presented. Subjects had to judge a total of 96 words. The basic principle for measuring ERD is that alpha shows a typical phasic change over the time course of a trial. After a response, the subject relaxes and awaits the presentation of the next stimulus. This state of relaxed but alert wakefulness is reflected by a pronounced alpha activity during the reference interval which precedes each trial. Even before the warning signal actually appears, the alpha rhythm becomes suppressed, because the subject anticipates the beginning of the next trial.

The measurement of ERD is done in several steps. First, the EEG is band pass filtered within defined frequency bands, the filtered data are squared and then averaged within consecutive time intervals (of e.g., 125 ms). Second, the obtained data are averaged over the number of epochs. Third, band power changes are expressed as the percentage of a decrease or increase in band power during a test as compared to a reference interval by using the following simple formula: $ERD = ((\text{band power reference} - \text{band power test}) / (\text{band power reference})) \times 100$. Note that desynchronization is reflected by positive ERD values, whereas event-related synchronization (ERS) is reflected by negative ERD values [122,124].

The appropriate selection of frequency bands is one of the most critical issues when using ERD or related measures such as changes in induced band power (IBP; cf.

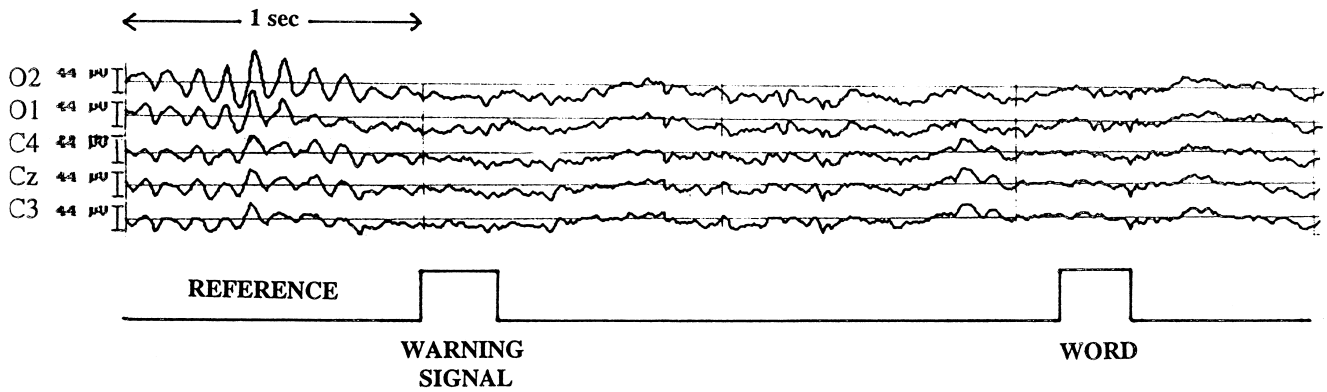


Fig. 7. Typical example of an EEG epoch, showing the basic principle of alpha desynchronization. During the first second of the epoch, which is called reference interval, the subject shows pronounced rhythmic alpha activity. Subjects run through many trials and, thus, the anticipation of the warning 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. 8).

Refs. [82,83]. Due to large interindividual differences of alpha frequency, large portions of alpha power may fall outside a fixed frequency window and invite misleading interpretations (cf. Fig. 1). In order to avoid these and related problems that arise with fixed frequency windows, we (e.g., Refs. [69,79–81]) suggested to use alpha frequency $f(i)$, averaged over all leads, as an anchor point to adjust frequency bands individually for each subject. Then, four frequency bands with a width of 2 Hz can be defined in relation to $f(i)$ that cover the traditional theta and alpha frequency range from about 4–12 Hz (depending on the actual $f(i)$ for each subject). The frequency bands obtained by this method are termed: theta ($f(i)-6$ to $f(i)-4$); lower 1 alpha ($f(i)-4$ to $f(i)-2$); lower 2 alpha ($f(i)-2$ to $f(i)$) and upper alpha ($f(i)$ to $f(i)+2$). For each subject, ERD is calculated within these individually determined frequency bands. We have shown in several studies that fixed frequency bands blur the specific relationships between cognitive performance and ERD, we otherwise are able to observe (as an example, see Fig. 11).

4.1. Desynchronization in the lower alpha band reflects attention

One of our most basic findings with respect to the alpha frequency range is that alpha desynchronization is not a unitary phenomenon. If different frequency bands are distinguished within the range of the extended alpha band, two distinct patterns of desynchronization can be observed. Lower alpha desynchronization (in the range of about 6–10 Hz) is obtained in response to a variety of non-task and non-stimulus specific factors [see also Refs. [45,163]] which may be best subsumed under the term ‘attention’ (for a similar concept, see Ref. [135]). It is topographically widespread over the entire scalp and probably reflects general task demands and attentional processes. Upper alpha desynchronization (in the range of about 10–12 Hz) is topographically restricted and develops during the pro-

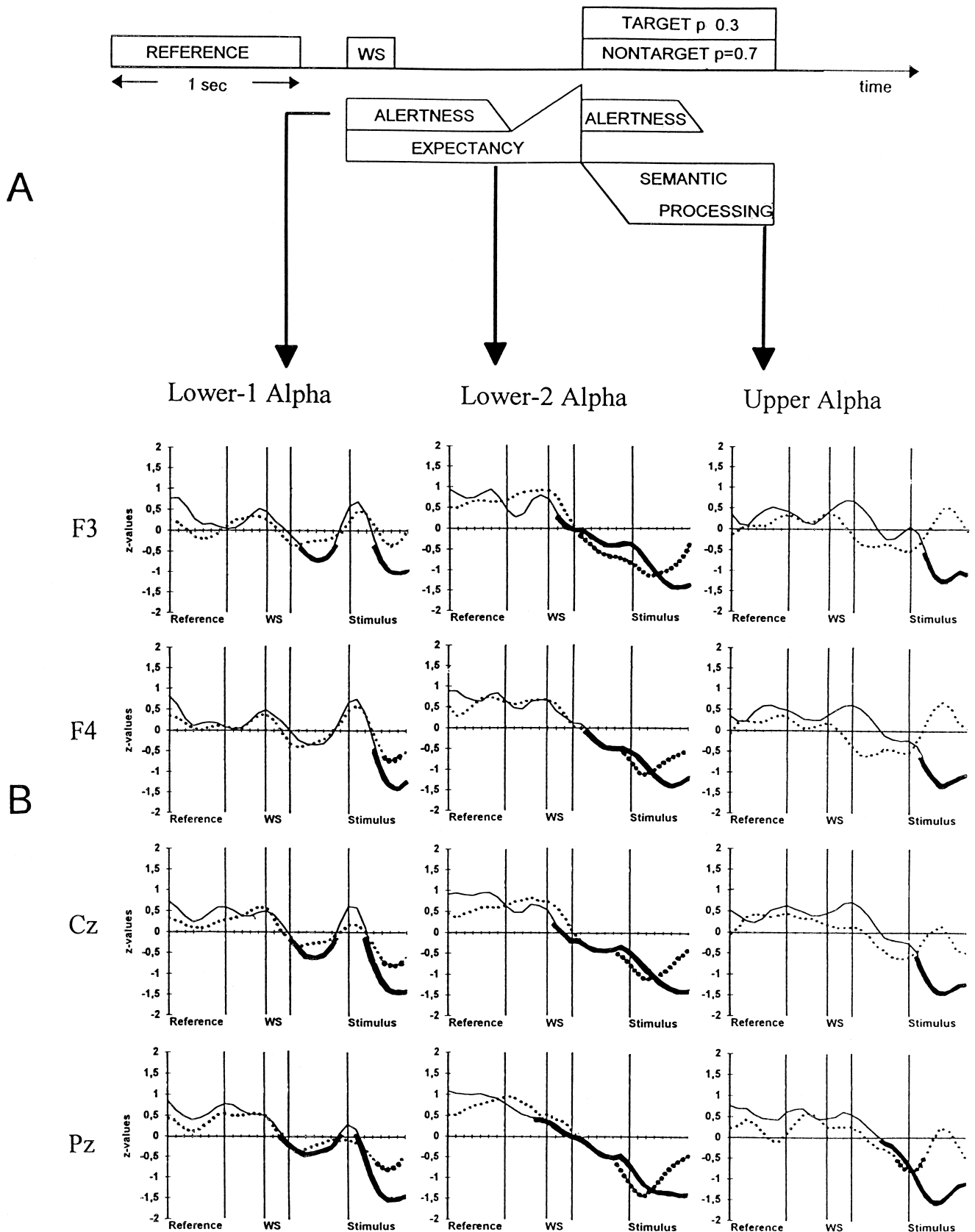
cessing of sensory-semantic information as recent evidence indicates (e.g., Refs. [72,75,78–81]).

The sensitivity of the lower alpha band with respect to attentional demands can be demonstrated by the results of a modified visual oddball task [83]. Two different components of attention, alertness (or arousal) and expectancy were studied (for a detailed cognitive analysis and definition of these terms, see Refs. [126,127]). In each trial a warning signal preceded the presentation of an imperative stimulus (target or nontarget). Subjects were asked to count the targets but to ignore nontargets. We assume that the warning signal and the target increase alertness and that the time before a target or nontarget appears reflects a state of increased expectancy. It is important to note that the presentation of targets and nontargets was not completely random. First, targets are rare and nontargets are frequent (the ratio is 30%:70%) and second, no more than three targets or nontargets were allowed to occur in succession. Thus, on the average, subjects were well able to expect (and make a good guess about) the occurrence of a target after a few trials. A large number of trials (200 stimulus presentations) was used to guarantee that subjects have enough time to get familiar with the sequence of targets and nontargets. Because it is well established that a variety of different components of event-related potentials (ERP’s) are sensitive to attentional demands (cf. Ref. [98]), we in addition wanted to show whether event-related band power changes that can be observed in response to attentional demands are due to ERP components. Thus, we used IBP which is a measure that does not contain evoked EEG activity [82].

As the results depicted in Fig. 8 demonstrate, a significant response (decrease in band power) to the warning signal can be observed only in the lower-1 alpha band and when the warning signal preceded a target (note that for IBP, desynchronization is indicated by negative z -values). The finding indicates that—on the average—subjects were able to predict (expect) the occurrence of a target and that

the warning signal exerts an alerting effect primarily if it precedes a target. This alerting effect is reflected by a decrease in band power that is interrupted and, thus,

separable from the decrease in band power that occurs in response to the imperative stimulus. In contrast to the lower-1 alpha band, a steady decrease in band power



starting as early as 1000 ms before the onset of an imperative stimulus—probably reflecting expectancy—was obtained in the lower-2 alpha band. Because expectancy plays a role during the prestimulus period of both types of stimuli, there is no reason to assume that the prestimulus period will differ between target and nontarget trials. After the appearance of the imperative stimulus, however, the processing of targets and nontargets will be different. If a target appeared, subjects expect still to perform another task which is to count targets and press the response key. Thus, during the poststimulus period, targets show a somewhat larger lower-2 alpha desynchronization than nontargets.

We have found repeatedly that the upper alpha band is most sensitive to semantic or task specific effects. Thus, the largest differences between targets and nontargets are expected for the upper alpha band and during the second half of the poststimulus interval when the stimulus type is recognized and subjects start to count. This is indeed the case as Fig. 9 indicates. The findings demonstrate that three alpha bands proved useful for a better distinction between different cognitive processes. Furthermore, they replicate and extend related findings in earlier studies [72–75].

4.2. Desynchronization in the upper alpha band reflects semantic memory performance

Based on earlier findings from our laboratory (e.g., Ref. [75]), we have suggested and tested the hypothesis that upper alpha desynchronization correlates with semantic memory performance whereas theta synchronization correlates with working memory or episodic memory performance in particular. In two recently performed experiments, Klimesch et al. [79] and in a partially modified replication study [80], subjects had to judge, whether sequentially presented feature-concept pairs (such as ‘claws—eagle’, ‘wings—banana’, ‘yellow—hawk’, ‘seeds—cucumber’ etc.) are semantically congruent. It is important to note that the semantic judgment cannot be carried out before the concept word is presented. Thus, upper alpha desynchronization is expected to be significantly larger during the processing of the concept as compared to the feature word.

The results as summarized in Fig. 9 indicate that the upper alpha band is specifically related to the processing of semantic information. The most important results are that a significant increase in upper alpha desynchronization was found only during that time interval in which the semantic judgment task actually was carried out (cf. $t5$ in Fig. 9) and that the theta band did not respond to semantic task demands at all. The two lower alpha bands exhibit a stepwise increase in desynchronization that exceeds the level of significance even before a semantic relationship between the feature and concept words can be detected and, thus most likely reflect the increase in attentional demands during the time course of the entire trial.

The increase in upper alpha desynchronization during the semantic task in $t5$ is strictly localized over the left hemisphere. This finding is well in line with a variety of PET-studies and Tulving’s HERA model [159]. As an example, Petersen et al. [120] have shown that semantic task demands (particularly the retrieval of semantic information) are associated with a pronounced increase in the blood flow at left prefrontal regions (see also Ref. [128]). In addition, Martin et al. [104] have found that naming pictures of animals and tools (parts of the words used in the present study also represent animals, others such as weapons were similar to tools) was associated with bilateral activation of the temporal lobes and the calcarine region, the left thalamus and the left anterior insula/inferior frontal region (cf. Fig. 1 in Ref. [104]).

In Klimesch et al. [80], after a judgment task, subjects performed a semantic and episodic memory task (see also [79]). The prediction was that upper alpha desynchronization should be larger for good as compared to bad semantic memory performers. In general, we expected that upper alpha desynchronization is related to semantic memory performance, whereas theta synchronization is related to episodic memory performance.

In the semantic and the episodic memory task, the (congruent) feature words of the judgment task were presented. In the semantic task, subjects were asked to report any association that comes into their minds. In the episodic memory task, they were instructed to report only that concept word that actually was paired with a feature word. In the semantic task too, only correct responses (e.g.,

Fig. 8. (A) Structure of a single trial in a modified visual oddball task (data from Klimesch et al. [83]). An alerting warning signal precedes an imperative stimulus (target or nontarget). Subjects are asked to count targets but to ignore nontargets. (B) The assumed sequence of cognitive operations. It is predicted that the lower-1 alpha band reflects phasic alertness and responds to the WS and (imperative) stimulus with a decrease in band power (desynchronization). The lower-2 alpha band reflects expectancy and desynchronizes before the imperative stimulus appears. The upper alpha band reflects semantic processes that are related to task performance and, thus, shows maximal desynchronization in the late poststimulus interval (for targets) only. (C) Time course of changes in induced band power (IBP) for targets (bold line) and nontargets (dashed line) in three alpha bands with a width of 2 Hz each. IBP represents z -transformed power. Negative values indicate desynchronization, positive values synchronization. The reference interval was used to calculate confidence intervals. Thus, significant changes (marked by extra bold segments) refer to differences between the reference interval and subsequent time periods. As the results indicate, the lower-1 alpha band shows a phasic response to the WS and imperative stimulus, whereas the lower-2 alpha band exhibits a tonic increase in desynchronization that starts already before a target and nontarget appears. The upper alpha band shows the largest difference between targets and nontargets. Note that maximal desynchronization occurs in the poststimulus period for targets only. The length of the reference interval is 1 s.

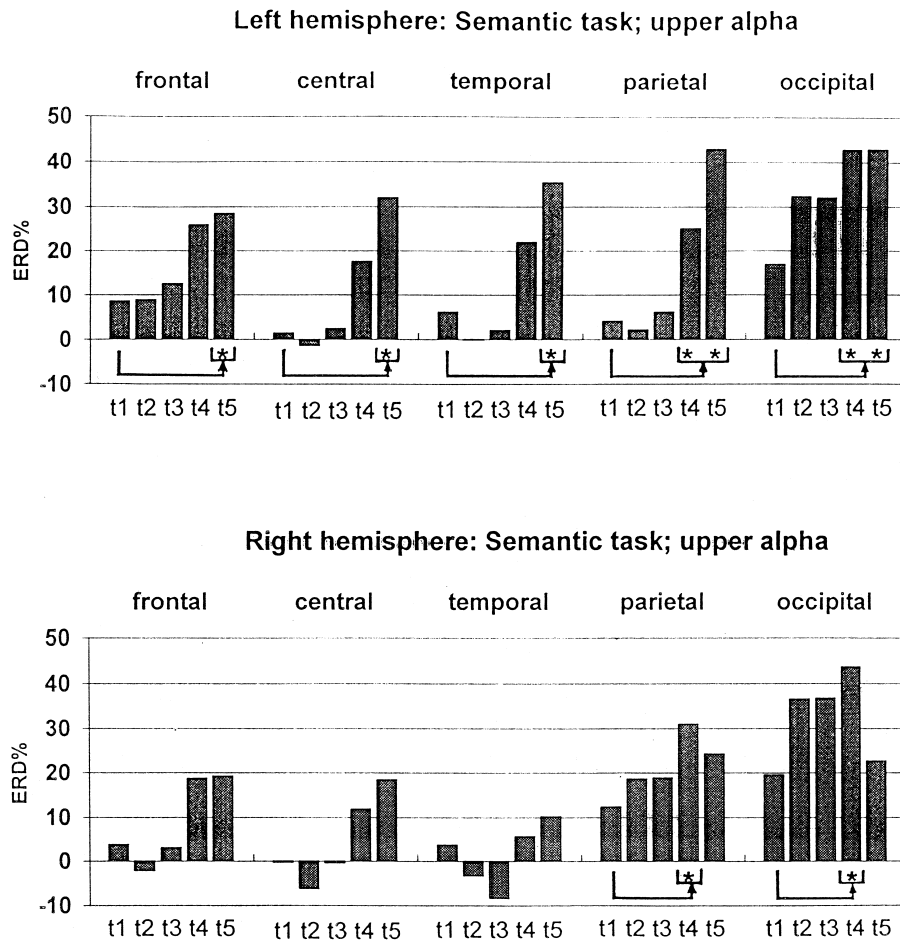


Fig. 9. Time course of event-related desynchronization (ERD) in the upper alpha band during a semantic judgment task [79]. Subjects had to judge whether a feature word (presented during t_2) is semantically congruent with a concept word (presented during t_4). Each interval (t_1 – t_5) represents a time period of 500 ms. The results show that upper alpha desynchronization (as measured by ERD) is largest during t_5 which is that time period in which the semantic judgment process actually takes place. Note the strong left hemispheric advantage (larger ERD-values over the left as compared to the right side of the scalp) particularly during t_5 .

‘eagle’ in response to ‘claws’) were counted. Thus, the only difference between the two tasks was the way subjects were instructed to retrieve information from their memory. In the semantic task, the number of correct responses was considered to reflect the strength of semantic associations. In the episodic task subjects had to focus on the specific pairing between a feature and concept. Because there are many different and semantically congruent ways a feature can be paired with a concept (e.g., ‘claws’ can also be paired with ‘hawk’) subjects had to retrieve the experimental context in which a particular feature was presented (i.e., was ‘claws’ presented in the context of ‘eagle’ or ‘hawk’?). Thus, the number of correct responses in this task was considered to reflect episodic memory performance. Subjects were divided into a group of good and a group of bad semantic memory performers. This was done on the basis of the semantic recall scores which were organized according to increasing values and were used to cut the sample into two halves. The results of this study shows again that in contrast to the theta and the two lower alpha bands, only the upper alpha responds to

semantic task demands. The most important finding of this study, however, was that upper alpha desynchronization during the semantic judgment process is significantly larger for good semantic memory performers as compared to bad performers, as Fig. 10 demonstrates. Furthermore, during the semantic judgment process, significant positive correlations were found between upper alpha desynchronization and semantic memory performance at frontal, central, temporal and parietal recording sites. Episodic memory was significantly correlated with theta synchronization. However, when the influence of episodic memory performance was removed by means of partial correlations, significant correlations between upper alpha desynchronization and semantic memory performance remained at frontal, central and parietal recording sites.

With respect to the relationship between upper alpha desynchronization and memory performance, similar findings were also obtained by Klimesch et al. [73] and Serman et al. [146] but of course not in studies using broad bands within fixed frequency limits (e.g., Ref. [132]). Finally, it should also be noted that some memory studies

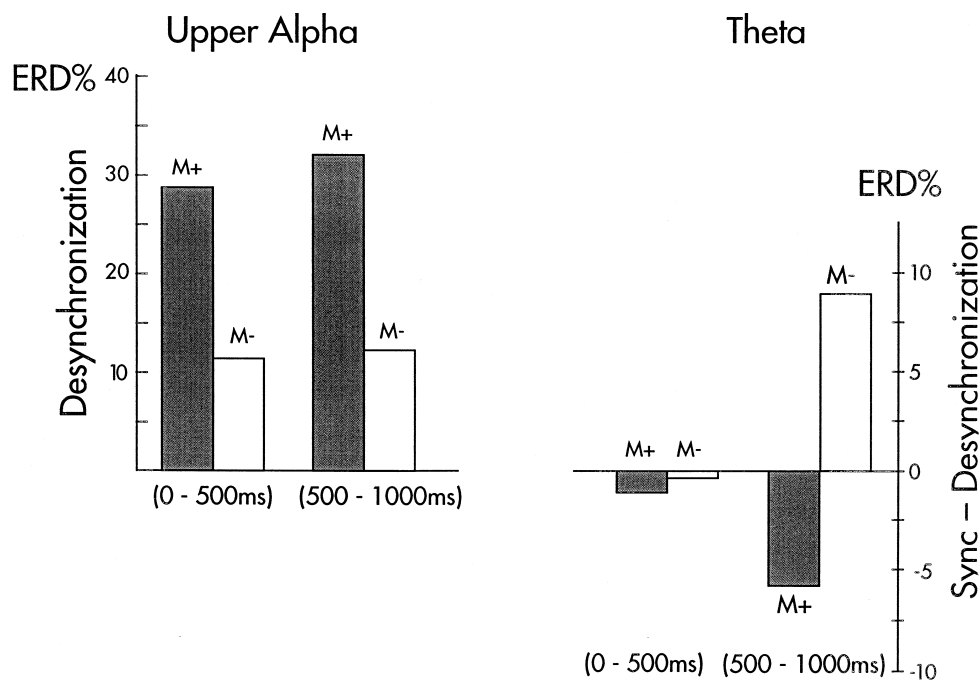


Fig. 10. Time course of event-related desynchronization (ERD) in the upper alpha and theta band during a semantic judgment task of the type used in Klimesch et al. [79], analysed separately for good (M+) and bad memory performers (M-) in a similar experiment [80]. Data are averaged for all recording sites. The time period of 0–500 ms corresponds to t_4 in Fig. 9, the period of 500–1000 ms poststimulus corresponds to t_5 in Fig. 9. The results indicate that in the upper alpha band, good memory performance (M+) is reflected by a significantly larger extent of desynchronization. The opposite holds true for the theta band where good memory performance is reflected by a larger extent of synchronization (expressed by negative ERD values).

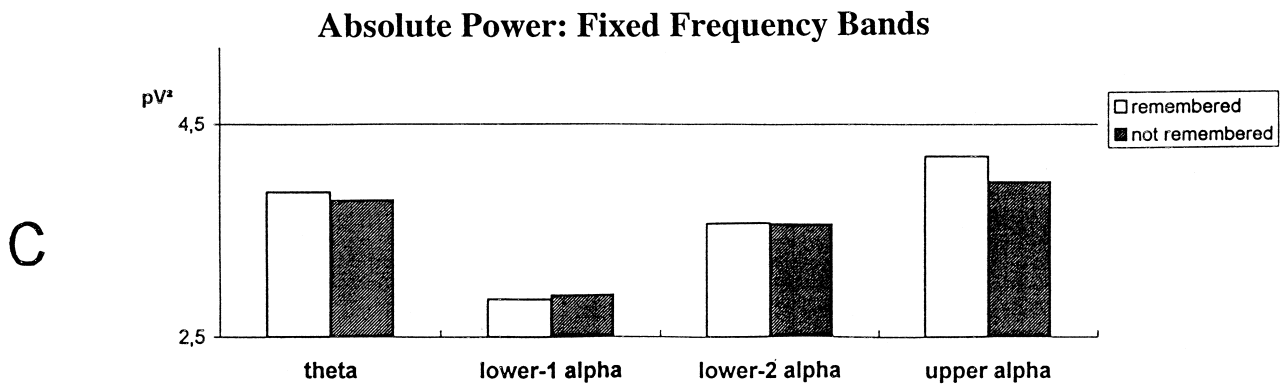
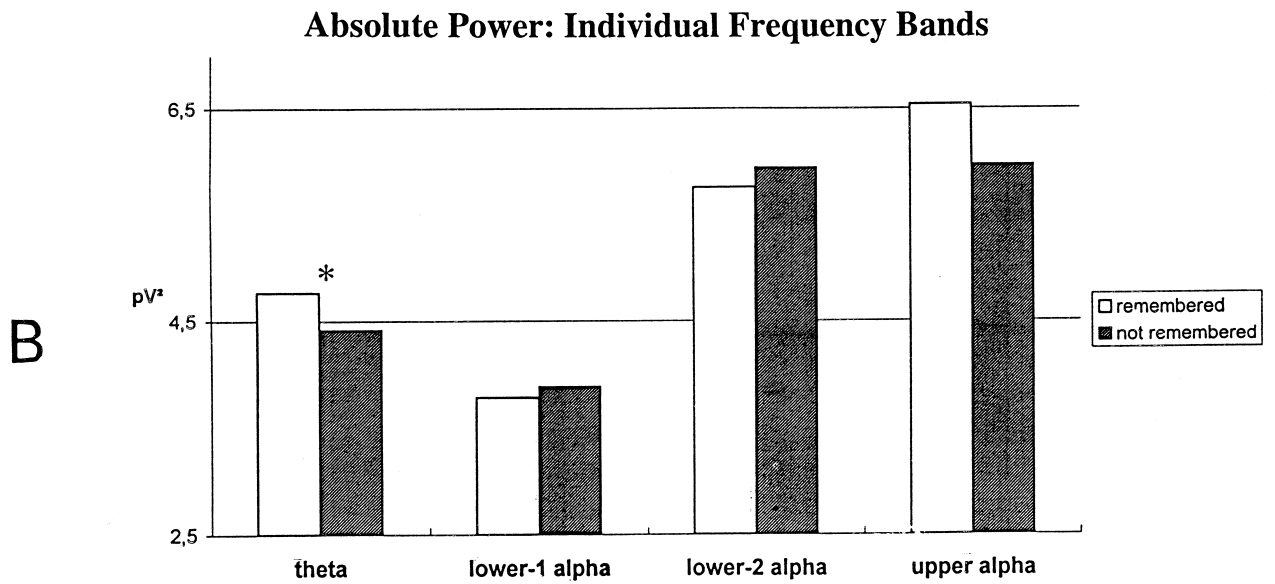
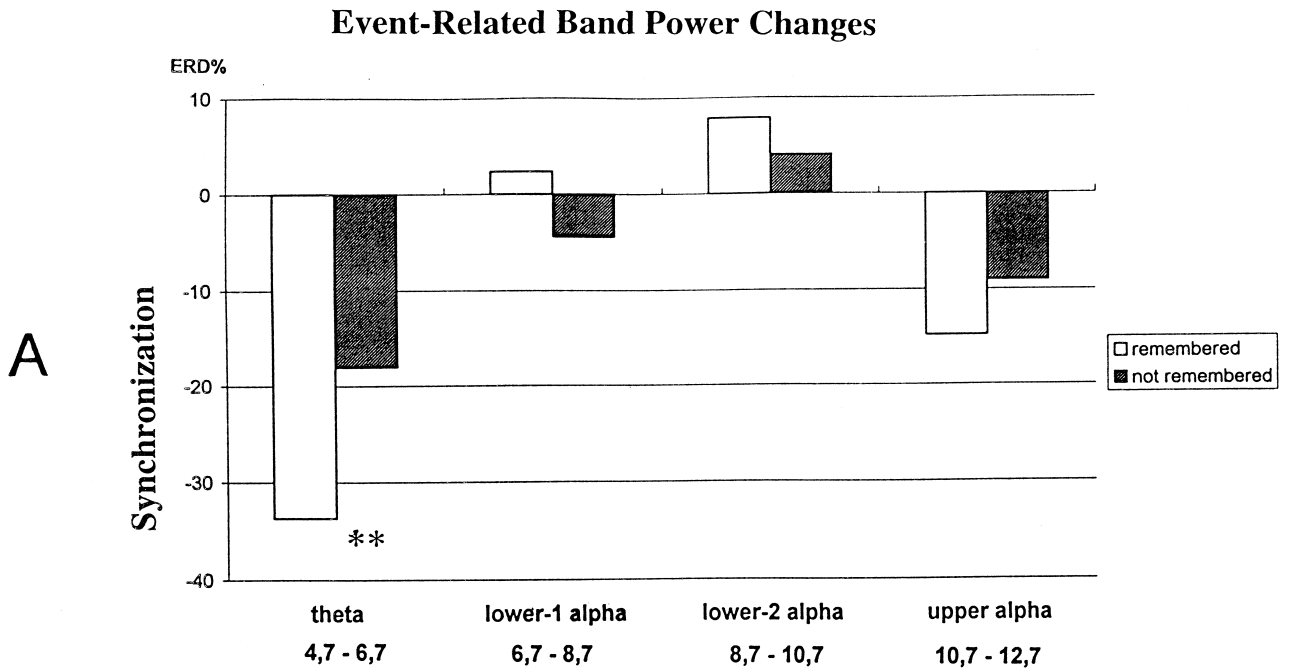
using narrow bands but acoustic stimuli (Krause et al. [89,90]) failed to replicate our findings. This failure is possibly due to the fact that simple tones such as Krause et al. used affect the tau rhythm which cannot be detected by scalp electrodes. Preliminary evidence for this view comes from an interesting study by Kaufman et al. [65] who found suppression of rhythmic activity in the alpha range over the auditory cortex when subjects scan memory for tones.

4.3. Synchronization in the theta band reflects episodic memory and the encoding of new information

Studies focusing on the hippocampal theta rhythm in animals have provided good evidence that theta power is related to the encoding of new information (cf. Refs. [20,107] for reviews) and to episodic memory in particular [47]. In a series of experiments, we were able to demonstrate that even in the human scalp EEG, the theta band responds selectively to the encoding of new information into episodic memory. This effect was first demonstrated by Klimesch et al. [75] and was meanwhile extended [45,46,76,79,81,163,168] and replicated by other research groups [18].

In the study by Klimesch et al. [76] the hypothesis was tested, whether a task related increase in theta power selectively reflects the successful encoding of new information. Because theta power increases in a large variety of different tasks (see e.g., the review in Ref. [133]) it seems

plausible to assume that theta power reflects—at least in part—unspecific factors such as e.g., attentional demands, task difficulty and cognitive load. Consequently, when trying to test the suggested hypothesis, it is important to use an experimental design which allows to control for unspecific factors. In Klimesch et al. [76], this was done by using an incidental instead of an intentional memory paradigm. During the encoding phase (i.e., the presentation of a series of words), subjects did not know that memory performance will be tested later. The crucial test for the proposed hypothesis was to calculate band power changes during the encoding stage and to compare words which can be remembered later with those which cannot be remembered later. If an increase in theta power is indeed related to a successful encoding of new information, it is to be expected that words which can be remembered in the later recall task show a significantly larger increase in theta power during encoding than words which will not be remembered later. Because all of the words used in the present study were very common, because semantic judgment tasks are very easy and because subjects did not know that their memory will be tested later, stimulus type, task difficulty, differences in mental load or specific encoding strategies can be excluded from the list of unspecific factors that influence the extent of theta synchronization. Thus, there are good reasons to assume, that the only difference between the later remembered and not remembered words refers to the actual establishment of a memory trace.



The results are plotted in Fig. 11 and demonstrate that words which could be remembered later exhibited a significantly larger extent of theta synchronization than not remembered words. Not only did theta synchronization reach significance, so did also absolute theta power, but only if frequency bands were adjusted individually. Similar findings were also obtained in a recognition task [81] where subjects knew that their memory will be tested later. Significant theta synchronization was found during the encoding phase for those words only which could be remembered later and only for correctly recognized targets during the actual recognition phase but not for distractors and not remembered targets.

4.4. The relationship between desynchronization, synchronization and absolute power

As the results by Klimesch et al. [75,76,79,80] have shown, the extent of theta synchronization and upper alpha desynchronization are related to episodic and semantic memory performance, respectively. Although these findings reveal very specific effects, they are in good agreement with the well known fact that the amount of alpha desynchronization generally is related to the relevance and/or difficulty of a task. The more demanding or relevant a task, the stronger the amount of alpha suppression or ERD (e.g., Refs. [69,14,73], cf. the review in Klimesch [68]). In a pure logical sense one would expect that the amount of desynchronization should depend on absolute power. Only if there is sufficient activity during a reference or resting interval would there be a possibility of a large extent of power suppression during task performance. A similar relationship may also be expected on the basis of physiological considerations. It would be quite plausible to assume that after a difficult task, a rebound of alpha activity takes place that lasts even into the reference interval of the next following trial (epoch). If this occurs trial after trial, the percentage of desynchronization (ERD) would clearly be linked to the power of the reference interval.

This issue was studied in a recent experiment by Doppelmayr et al. [35]. For all of the three alpha bands, the results clearly indicate that large band power in the reference interval is associated with a large amount of desynchronization (alpha suppression) during task performance. Most interestingly, the opposite holds true for the theta band. Here, small reference power is related to a large amount of synchronization or increase in power. Thus, the extent of alpha desynchronization and theta synchroniza-

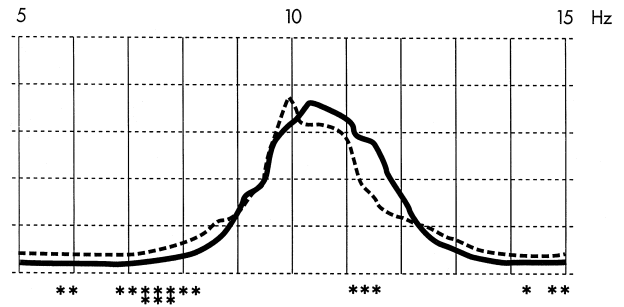


Fig. 12. Normalized percent power for good (bold line) and bad memory performers (dotted line) during memorizing words at O1 [84]. The ongoing EEG was analysed for 4 min and arbitrarily segmented in epochs of 4 s in order to achieve a frequency resolution of 0.25 Hz. Significant results (of *t*-tests between good and bad memory performers) are marked by one asterisk (for the 5%-level) or two vertically arranged asterisks (for the 1%-level). Good memory performers show significantly more upper alpha but less theta power. Similar results were found for all recording sites and even during resting sessions with eyes open and closed.

tion depend on the magnitude of absolute band power, but in opposite ways. With respect to the broad alpha band (7–14 Hz), similar findings were reported by Salenius et al. [132]. The interesting conclusion, thus, is that the reactivity in band power which reflects task performance can be predicted from the amount of absolute power as measured during a resting state.

With respect to the relationship between memory performance and absolute power, the reported findings allow us to make an important prediction. We would expect that good as compared to bad memory performers show significantly more power in the upper alpha but less power in the theta band. This result would be expected even when the EEG is measured during a resting phase. This hypothesis was clearly supported by two recent studies [161,84], as the example shown in Fig. 12 indicates. Similar findings were reported by Jausovec [61]. He found that highly intelligent subjects have significantly more absolute power in the broad alpha frequency range (7.5–13 Hz) than less intelligent subjects.

5. General conclusions and physiological considerations

The most important conclusion is that the amount of EEG power in the theta and alpha frequency range is indeed related to cognitive and memory performance in particular, if a double dissociation between absolute and event-related changes in alpha and theta power is taken

Fig. 11. ERD during the encoding phase of an incidental memory task, where subjects did not know in advance that a recall test will be carried out later. Data represent the time period of 1000 ms poststimulus after presentation onset of a word during encoding and are averaged over all recording sites. (A) Those words that can be remembered in a later recall task show a significantly larger task related increase in theta power (negative ERD values) during encoding as compared to words that cannot be remembered later. The respective differences in the three alpha bands are not significant. (B) In the theta band not only (negative) ERD (reflecting the percentage of an increase in power with respect to a reference interval) but also absolute power too is significantly larger for remembered words but only if frequency bands are adjusted individually (as for the ERD analysis) to IAF (cf. Fig. 1). (C) If instead fixed frequency windows are used, no significant differences can be observed. Data from Klimesch et al. [76].

into account. This double dissociation is characterized by the fact that during a resting state

- (i) small theta power but large alpha power (particularly in the frequency range of the upper alpha band) indicates good performance, whereas the opposite holds true for event-related changes, where
- (ii) a large increase in theta power (synchronization) but a large decrease in alpha power (desynchronization) reflect good cognitive and memory performance in particular.

A comparison with findings about the hippocampal theta rhythm in animals reveals that in response to increasing encoding demands, hippocampal theta synchronizes in a small frequency window, just as the human theta (scalp) EEG does (for an extensive review of this issue see Ref. [67]). Theta synchronization is due to an increase in the duration of multi-unit population bursts and to an increase in rhythmicity of these bursts which have the same frequency as theta. Convincing evidence for the hypothesis that theta synchronization is related to the encoding of new information comes from the fact that LTP is closely linked to the synchronous activity of the hippocampal theta rhythm:

- LTP can be best induced with stimulation patterns that mimic theta rhythm [92].
- LTP has been demonstrated in several brain regions, but it is most robust and, thus, has been studied most extensively in the hippocampus (c.f. Ref. [100]).
- The induction of LTP occurs primarily during the positive phase of the theta rhythm [119].
- The strength of the induced LTP increases linearly with increasing theta power ([100] c.f. Fig. 6 on p. 50).
- Pharmacological manipulations demonstrate that drugs which decrease theta activity also block learning [48], whereas drugs that promote the theta rhythm (and, thus, enhance the induction of LTP) also facilitate learning [142,143].

These findings support the view that hippocampal theta is important for the induction of LTP and is related to the encoding of new information in a similar way as LTP is. Consequently, we may assume that our results (e.g., Refs. [75,77,80,81] which suggest a close relationship between theta synchronization and the encoding of new information reflect theta activity that is induced into the cortex via cortico-hippocampal feedback loops (cf. Ref. [107] for a comprehensive review on this topic). Further evidence for this interpretation comes from an interesting study by Gevins et al. [46], who used a new method to spatially sharpen the EEG with magnetic resonance imaging-based finite element deblurring. These authors found a frontal midline theta rhythm which increased with increasing memory load. Most interestingly, dipole models localized this signal to the region of the anterior cingulate cortex which is part of the Papez circuit and, thus, is linked with the hippocampal formation via complex feedback or 'reentrant' loops.

It should be noted that there are two different types 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 irregular slow activity (ISA) which also is termed large irregular activity (LIA). Irregular slow activity dominates during slow wave sleep (SWS) and shows increased power outside the theta peak range (cf. Ref. [93]). This type of synchronization is not related to the increased power of a dominant rhythm within a narrow frequency band, but rather to an increase in power over a broad range. It may be explained in terms of irregular oscillatory epochs of the type Buzsaki et al. [19] have described. These irregular oscillatory epochs which occur over a comparatively broad frequency range are not coupled to the 'coordinating' force of the theta rhythm and are not related to the encoding of new information. It appears plausible to assume that the broad band increase in theta power reflects a state in which the ability to encode new information is reduced or even blocked (e.g., during the hypnagogic state, in SWS or in demented subjects) whereas the narrow band synchronization during regular rhythmic theta activity reflects event-related theta synchronization that is closely linked to the encoding of new information (or 'recoding' during REM).

In contrast to theta, the physiological mechanisms underlying alpha desynchronization appear more complex and at the first glance even paradoxical. Whereas alpha synchronization occurs during alert wakefulness, desynchronization reflects actual cognitive information processes. Alpha synchronization is a state in which millions of cortical neurons oscillate synchronously with the same phase and within a comparatively narrow frequency band. Desynchronization seems to imply that different oscillators within the alpha band are no longer coupled and start to oscillate with different frequencies. These different oscillators most likely reflect the synchronous activity of more local cortical or thalamocortical networks [97] and are, thus, termed 'local' or 'functional' alphas [7,8,114,115]. For each of the local alphas all neurons may still show a regular pattern of synchronous oscillation.

This basic EEG-phenomenon of large scale alpha synchronization (during mental inactivity) and desynchronization (during mental activity) which probably reflects a complex pattern of micro scale synchronization provides us with a preliminary but nonetheless important understanding of how information may be processed in the brain: Large scale alpha synchronization blocks information processing because very large populations of neurons oscillate with the same phase and frequency. In contrast, alpha desynchronization reflects actual cognitive processes because different neuronal networks start to oscillate at different frequencies and with different phases.

Research focusing on gamma oscillations in the visual cortex have shown that synchronous oscillatory discharge patterns reflect an elementary visual encoding process

(e.g., Ref. [49]). These results, obtained with microelectrodes, are a good example of a microscale synchronization. With respect to the human scalp EEG, it is a matter of resolution, whether or not we may speak of synchronization or desynchronization. Even if the EEG desynchronizes, a large number of different networks may still show synchronous oscillations on a microscale level. In order to discriminate between these two different types of synchronization, the synchronous activity of large cortical areas reflecting mental inactivity is termed type 1 synchronization, whereas the regular synchronous oscillatory discharge pattern of selected and comparatively small cortical areas is termed type 2 synchronization [67]. 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 rather weak signal for the human scalp EEG. Thus, the behavior of the alpha rhythm can be explained by type 1 synchronization reflecting mental inactivity and type 2 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 general conclusion, thus, is that regular type 2 synchronization is that oscillatory mode in all of the frequency bands that reflects actual information processing in the brain.

In an attempt to integrate results from memory research in divergent fields such as cognitive psychology, neuroanatomy and neurophysiology, Klimesch [67] has suggested that type 2 synchronization, generated by thalamo-cortical and cortico-cortical feedback loops (cf. Refs. [144,97,91]) provides an ideal framework for describing spreading activation processes in semantic long-term memory. Thus, it may be assumed that type 2 synchronization as measured by (upper) alpha desynchronization reflects search and retrieval processes in semantic long-term memory which are induced into the cortex by thalamo-cortical feedback loops. For the theta band it is suggested that hippocampo-cortical pathways induce synchronous oscillations within a narrow frequency window of the theta peak into widely distributed assemblies in the cortex, thereby binding different parts of cell assemblies together. This binding process forms the basis for encoding new information (for similar conceptions, see also Refs. [107,94]). This interpretation also implies that cognitive performance is closely linked to type 2 synchronization in thalamo- and hippocampo-cortical networks.

Acknowledgements

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