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## Review

# EEG alpha oscillations: The inhibition–timing hypothesis

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### ABSTRACT

The traditional belief is that the event-related alpha response can solely be described in terms of suppression or event-related desynchronization (ERD). Recent research, however, has shown that under certain conditions alpha responds reliably with an increase in amplitudes (event-related synchronization or ERS). ERS is elicited in situations, where subjects withhold or control the execution of a response and is obtained over sites that probably are under, or exert top-down control. Thus, we assume that alpha ERS reflects top-down, inhibitory control processes. This assumption leads over to the timing aspect of our hypothesis. By the very nature of an oscillation, rhythmic amplitude changes reflect rhythmic changes in excitation of a population of neurons. Thus, the time and direction of a change – described by phase – is functionally related to the timing of neuronal activation processes. A variety of findings supports this view and shows, e.g., that alpha phase coherence increases between task-relevant sites and that phase lag lies within a time range that is consistent with neuronal transmission speed. Another implication is that phase reset will be a powerful mechanism for the event-related timing of cortical processes. Empirical evidence suggests that the extent of phase locking is a functionally sensitive measure that is related to cognitive performance. Our general conclusion is that alpha ERS plays an active role for the inhibitory control and timing of cortical processing whereas ERD reflects the gradual release of inhibition associated with the emergence of complex spreading activation processes.

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## 1. Introduction: basic principles underlying the inhibition–timing hypothesis

Oscillations reflect rhythmic changes in the (relative) level of depolarization in the (dendritic and somatic) membrane potentials of masses of neurons. Consequently, they reflect phases of low versus high excitability. The basic principle (shown in Fig. 1) can be illustrated by considering the phase of oscillatory activity together with the level of excitation in excitatory neurons. For simplicity, we assume that oscillatory activity is induced by inhibitory cells and reflects rhythmic changes between phases of maximal and minimal inhibition. Depending on the excitation level of pyramidal cells, two different firing patterns can be distinguished. A cell may fire tonically if its excitation level is high enough to override the influence of inhibition (cf. cell 1 in Fig. 1A) or it may fire rhythmically (entrained to the oscillation) if either its excitation level is low (cf. cell 2 and 3 in Figs. 1A, B) or the amplitude of the oscillation is large (cf. cell 1 in Fig. 1B). An important aspect thereby is that an increase in amplitude (reflecting an increase in inhibition) may not lead to a general suppression of firing but to increased rhythmic activity (cf. Fig. 1B in contrast to Fig. 1A) and thereby to a more precise timing of neural activity because the oscillation provides only a small time window for firing for many neurons (for a recent review cf. Fries, 2005). Rhythmic synchronization between neurons will have a strong impact on common target cells, because they will receive neural activity synchronously. This model will serve as guideline for the discussion of the functional meaning of alpha activity.

The generators of alpha are not known yet. Thus, the question, whether alpha is induced by inhibitory activity and/or other factors such as network—or resonance properties or intrinsic properties of (certain populations of) neurons is still a matter of debate. But considering the fact that about 15% of cortical cells are GABAergic (Braitenberg and Schüz, 1991) and that only 10% of synchronously active neurons are capable of generating an amplitude which is about 10-fold of that of not

synchronized neurons (Elul, 1972), EEG alpha may – in theory – stem from rhythmic fluctuations of inhibitory neurons.

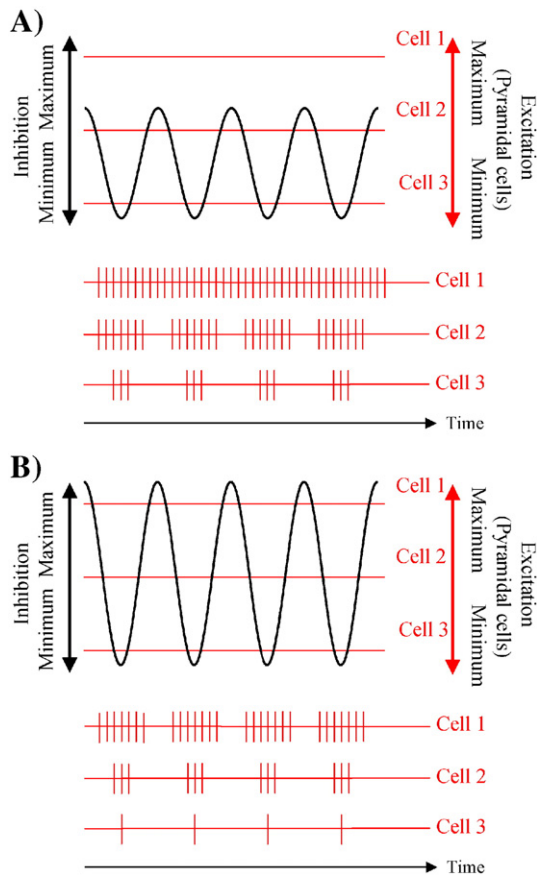
It is important to note that our considerations do not depend on whether alpha actually is induced by inhibitory neurons. The reason is that any EEG oscillation reflects rhythmic changes between phases of comparatively low versus high excitability, regardless of the factors that induce this oscillation.

As a working hypothesis and in contrast to the traditional view, we suggest that alpha oscillations play an important role during synchronized rhythmic activity that is similar for the pre- and poststimulus period, evoked and induced alpha. Two different aspects are distinguished, one is related to the state of brain activation, the other to the timing of information processing. We assume that desynchronized alpha activity (with small amplitudes in the scalp EEG) reflects a state of comparatively high excitability, whereas synchronized alpha activity (with large amplitudes in the scalp EEG) reflects a state of inhibition (comparatively low excitability). An important aspect thereby is that during the inhibitory state certain types of cognitive processes are enabled that reflect the control of a certain class of top-down processes. In the first part of the review (Section 3), we focus on alpha with respect to its meaning for the state of brain activation. In the second part (Section 4) we will discuss evidence for the timing of neural activity. Because very little is known about the physiology of alpha in the human brain we focus primarily on functional–behavioral correlates of human alpha and their interpretation. Nonetheless, in the final part of the review, we try to outline some basic aspects of the physiology of alpha activity.

## 2. Alpha and the state of brain activation

### 2.1. Alpha desynchronization (ERD) as a functional correlate of brain activation

The well-known alpha response – power suppression during eyes opening (described since the early days of EEG research,



**Fig. 1 – The basic principles underlying the inhibition-timing hypothesis can be illustrated by considering the phase of oscillatory activity together with the level of excitation of single neurons. We assume that oscillatory activity is induced by inhibitory cells and reflects rhythmic changes between phases of maximal and minimal inhibition. Depending on the amplitude of the oscillation (and the excitation level of single cells), two different firing patterns can be distinguished. (A) If the amplitude of the oscillation is small, cells with a high level of excitation fire tonically, not entrained to the phase of the oscillation. (B) If the amplitude is large even cells with a high level of excitation will fire rhythmically, entrained to the phase of the oscillation. Thus, increased rhythmic activity allows for a more precise timing of neural activity.**

cf. Berger, 1929) – suggests that light stimulation (bottom-up processing) is responsible for the decrease of the large amplitudes which can be observed particularly at posterior recording sites during closed eyes. Most interestingly, this interpretation is questioned by the simple fact that alpha suppression can also be observed solely in response to eyes opening (a top-down activation process) without visual stimulation in a completely dark room (cf. Moosmann et al., 2003 for a recent report). Thus, already this basic finding demonstrates that alpha suppression may not primarily reflect bottom-up sensory processing but rather may have been triggered by top-down processes. This conclusion is supported by the fact that – depending on the type of task demands – alpha suppression can also be observed over

frontal brain areas, particularly during the processing of semantic information (Klimesch et al., 1997a; cf. Klimesch, 1999 for a review).

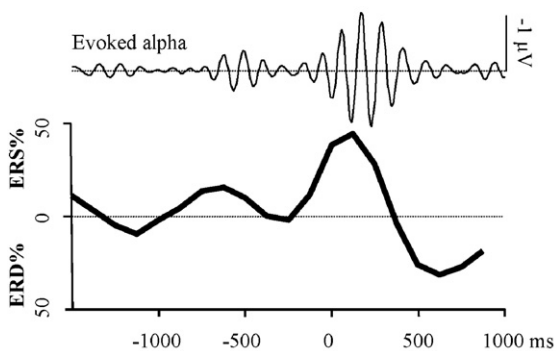
Alpha suppression, interpreted in terms of ‘desynchronization’, suggests that during information processing large populations of neurons no longer oscillate in synchrony. Thus, event-related desynchronization (ERD), calculated as the percentage of a band power change during the performance of some kind of task with respect to a reference or ‘resting’ interval (Pfurtscheller and Aranibar, 1977), may be considered a measure reflecting the extent to which synchrony is lost. In referring to the model as outlined above, this means that neurons no longer fire synchronously, i.e., entrained to alpha oscillations (cf. Fig. 1). The most basic findings from research on alpha ERD can be summarized as following. (i) ERD (in the extended alpha frequency range of about 7–13.5 Hz) can be observed in response to a variety of different types of tasks (for an extensive review cf. Pfurtscheller and Lopes da Silva, 1999). (ii) Alpha ERD is not a unitary phenomenon. Different frequency bands show a very distinct type of task-related reactivity and topography. Lower alpha ERD (in the range of about 7–10 Hz) is topographically widespread over the entire scalp, its functional meaning is less clear, probably related to general attentional demands. Upper alpha ERD (in the range of about 10–13.5 Hz) is topographically much more restricted and shows a clear relation to semantic processing demands (Klimesch et al., 1992, 1994, 1997a,b; Doppelmayr et al., 2002; cf. also the review in Klimesch, 1999). (iii) The time course of ERD – in response to a stimulus – depends very much on the type of task, frequency band and stimulation, but shows three typical features, a comparatively late onset at about 200 ms poststimulus (e.g., Klimesch et al., 2001), a desynchronization peak (maximal ERD) around 350–650 ms (cf. Fig. 2) and a resynchronization peak (increase in alpha) between about 900 ms and 2000 ms (e.g., Woertz et al., 2004; Serman, 1996). (iv) As depicted in Fig. 2, the late onset of ERD is due to evoked alpha that may even lead to a transient increase in alpha amplitudes (cf. Fig. 2A). (v) The duration of ERD is closely related to the duration of a task (Kaufman et al., 1990, 1992; Michel et al., 1994).

These and other findings (e.g., about the relationship between ERD, cognitive performance and intelligence) demonstrate clearly that a decrease in alpha band power (particularly in the upper frequency range) is functionally closely related to active cognitive processing. Thus, we may conclude that ERD reflects active information processing in the sense of excitatory brain processes. In the following section, we will show that in contrast to ERD, event-related synchronization (ERS) reflects inhibition.

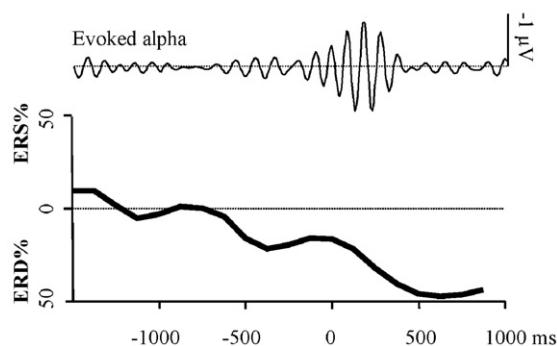
## 2.2. Alpha synchronization (ERS) as a functional correlate of inhibition in cognitive and motor tasks

The idea that large amplitudes of synchronized alpha activity reflect a brain state of reduced information processing (e.g., Pfurtscheller, 2001) is consistent with the concepts of ‘idling’ or ‘nil working’ (Adrian and Matthews, 1934) which were suggested in early EEG research. The concept of inhibition, however, was developed much later and was based on two different types of empirical evidence. Synchronized alpha

**A)** Lower alpha; 8–10 Hz; O1 correctly remembered pictures



**B)** Upper alpha; 10–12 Hz; O1 correctly remembered pictures



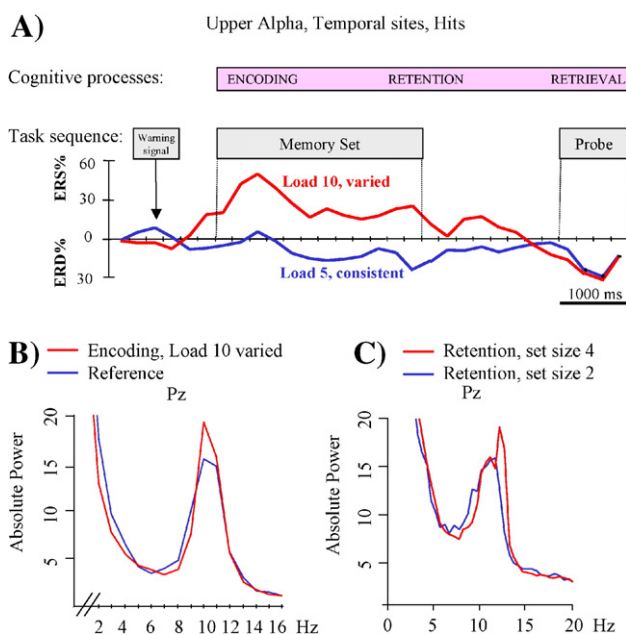
**Fig. 2** – The relationship between evoked power and ERD in a picture recognition memory task (unpublished results from the EEG data base reported in Klimesch et al., 2004). During a period of about 0–300 ms poststimulus, pronounced evoked alpha activity can be observed in the lower (A) and upper alpha band (B). We assume that in this early time window, the event-related alpha response is characterized by phase locking and – in most cases – by a transient increase in amplitudes (cf. also Fig. 7). Due to anticipation, alpha desynchronization may occur already before a stimulus is presented (B). Note the late desynchronization ‘peak’ at about 600 ms.

activity can be observed selectively (i) in tasks where a learned response must be withheld and (ii) over brain areas that are not task-relevant.

### 2.2.1. Tasks that induce ERS

Only more recently it became clear that certain task demands reliably induce ERS. A good example is a memory scanning task, where – during a retention interval – a subject (after encoding a certain number of items) has to keep the encoded information in mind and is instructed not to respond before a probe item is presented. In this type of task pronounced ERS can be observed during retention (Klimesch et al., 1999; Jensen et al., 2002; Schack and Klimesch, 2002; Busch and Herrmann, 2003; Cooper et al., 2003; Herrmann et al., 2004a; Sauseng et al., 2005b) but a strong ERD during retrieval, i.e., after the presentation of a probe (cf. Fig. 3). In addition, as depicted in Fig. 3A, when memory load is varied, alpha power increases as a function of the number of items to be remembered (Klimesch et al., 1999; Jensen et al., 2002; Schack and Klimesch,

2002). We (Klimesch et al., 1999) have interpreted these findings in terms of inhibition and as evidence against the idling hypothesis (cf. Pfurtscheller et al., 1996 for a review). For the interpretation of alpha ERS, it is important to consider the fact that in memory scanning tasks items of the memory set either remain the same over trials (consistent condition) or vary between trials (varied condition). Only in the varied condition subjects have to make sure to block retrieval of items from previous trials to avoid interference with the encoding and retention of new items. Our assumption is that alpha ERS reflects inhibitory top-down control to block retrieval of items from previous trials. Consistent with this interpretation, Fig. 3 shows that only in the varied condition ERS can be observed already during encoding. Then, with the



**Fig. 3** – Alpha power increases with memory load during encoding and retention in memory scanning tasks. (A) In a modified Sternberg task, a string of 5 or 10 characters (e.g., 2CF5R81H4L) was presented for 3000 ms (Klimesch et al., 1999). Then, after 2000 ms the probe item appeared (e.g., 3) and subjects had to indicate whether the probe item was contained in the memory set. In the most difficult condition (Load 10, varied) a new memory set was presented at each trial. Thus, probably because subjects tried to inhibit interfering memories of the preceding trial, alpha power increased already during the encoding of the memory set. The increase in alpha-compared to a reference interval preceding the presentation of a warning signal-reached almost 60%. Note that in contrast to encoding and retention, alpha exhibits a consistent ERD (decrease in power) during retrieval. (B) The increase in alpha is most pronounced in the upper alpha band and clearly visible in the power spectrum of the EEG. (Panels A and B are reprinted from Klimesch et al., 1999, with permission from Elsevier). (C) During the retention interval (1800 ms) of a memory scanning task with number words as items, alpha power increases with memory load (unpublished results from the EEG data base reported in Schack and Klimesch, 2002).



onset of retrieval, during the presentation of the probe, a strong ERD can be observed. [Gevins et al. \(1997\)](#) reported ERD with increasing working memory load. However, it should be emphasized that they used a n-back task in which information has to be updated and encoded, retained and retrieved in parallel. As we would only expect ERS during retention when retrieval of information should be blocked it is well in line with findings cited above that in a task requiring retrieval of information ERD is obtained.

The suggested interpretation is well in line with findings about motor behavior. Probably the most convincing evidence for the inhibition hypothesis was obtained by [Hummel et al. \(2002\)](#) who used a motor task in which subjects had to withhold a response. In addition, transcranial magnetic stimulation (TMS) was applied to assess cortical excitability. In response to visual cues subjects had to perform sequential finger movements on an electrical keyboard. Depending on the experimental condition, the task was either to actually perform the movements (ACT condition) or to look at the cues but to inhibit a response (INH condition). For the EEG experiment ERD in the upper alpha range (11–13 Hz) – reflecting the mu rhythm – was observed during ACT but ERS during INH. The separately performed TMS experiment in which pulses were applied over the primary motor cortex revealed that the amplitude of the motor evoked potential (MEP) at the hand was reduced during INH as compared to ACT and a baseline condition. Furthermore, patients with idiopathic dystonia (a disease with muscle cramp symptoms that most likely stem from deficient inhibitory circuitry) did neither show an amplitude reduction in the MEP nor ERS during INH.

These findings strongly suggest that increased oscillatory alpha activity reflects the inhibition to retrieve stored motor memory traces. This interpretation also is supported by the following additional findings. (i) ERS during INH was observed only if subjects were trained for the motor task in a preceding session but not in a control experiment without a training session. (ii). In a recent follow-up study, [Hummel et al. \(2004\)](#) have demonstrated that the blood oxygenation level-dependent (BOLD) signal decreases during INH. This is additional evidence that suppression of learned motor responses is associated with active inhibition. (iii) During motor imagery – which requires to retrieve a memory trace – ERD was observed only over the contralateral areas of the homunculus (which is involved in the storage of the relevant memory trace), but ERS over the ipsilateral side (which is not involved in the storage of the relevant memory trace; cf. [Neuper et al., 1999; Pfurtscheller and Neuper, 1997](#)).

The reactivity of the mu rhythm can be interpreted analogous to that of upper alpha in traditional memory tasks, in which upper alpha ERD is particularly large during retrieval over parietal areas which most likely are closely related to the storage of semantic and episodic memory traces ([Klimesch et al., 2006](#)). On the other hand, during retention (when information must not be retrieved), ERS can be observed over parietal areas (e.g., [Schack et al., 2005](#)).

## 2.2.2. ERS over brain areas that are not task-relevant

Research on ERD in cognitive tasks has shown very early that task-relevant brain areas exhibit ERD whereas areas not

relevant for the task either exhibit ERS or at least a smaller extent of ERD (cf. [Pfurtscheller and Klimesch, 1991; Worden et al., 2000; Foxe et al., 1998; Sauseng et al., 2005c](#)).

Convergent evidence also comes from studies about motor behavior and the mu rhythm. The interesting observation here is that during motor performance ERD is obtained over the respective areas of the homunculus, whereas ERS is observed over surrounding areas (cf. the concept of focal ERD/surround ERS described by [Pfurtscheller and Neuper, 1994](#)) and other more distant areas that are not task-relevant. It is important to note that this topographical distinct pattern of ERD/ERS that also is termed antagonistic ERD/ERS ([Neuper and Pfurtscheller, 2001](#)) is specific for the upper alpha frequency range. As suggested by [Suffczynski et al. \(2001\)](#), focal ERD reflects activation but surround ERS reflects the inhibition of neighboring cortical areas.

## 2.3. Further evidence for the inhibition hypothesis

In addition to the evidence reviewed in the previous sections, synchronized alpha activity can also be observed after a pronounced alpha suppression has occurred and during a reference or resting period. In the following we will show that these well-known basic aspects of alpha activity may also be interpreted in terms of inhibition.

### 2.3.1. ERD and resynchronization: cyclic changes between excitatory and inhibitory processes?

Besides ERS – as a specific task and processing-related increase in alpha – there is yet another type of power increase that typically can be observed after a task has been executed. First, in response to the presentation of a stimulus and/or a task alpha desynchronizes and reaches a desynchronization peak (maximal ERD) around 350 – 650 ms (or later, depending on the type and duration of the task). Then, after task execution, alpha power increases and reaches a synchronization peak up to several seconds later. As an example, with simple light stimulation (eyes open), maximal ERD can be found at about 500 ms and ERS between 1000 and 1500 ms ([Woertz et al., 2004](#)). Vanni and colleagues showed data for one subject with a strikingly different time course for non-objects and (correctly) recognized objects ([Vanni et al., 1997](#)). For non-objects the desynchronization peak is small with a short latency of about 350 ms, whereas resynchronization is large (also with an early latency of about 1100 ms). For objects the desynchronization peak is large but latency long (about 500 ms) whereas resynchronization is small (also with a long latency of about 1500 ms). The general role apparently is that a small desynchronization peak has a short latency and is accompanied by large and early resynchronization. A large desynchronization peak on the other hand has a long latency and is accompanied by a small and late resynchronization ([Woertz et al., 2004](#)).

Within the context of the suggested inhibition hypothesis our interpretation is that after extensive cortical excitation (reflected by a large desynchronization peak with long latency) it takes a while until inhibition (reflected by resynchronization) returns. On the other hand, after a less extensive and short lasting period of cortical excitation (reflected by a small desynchronization peak with short latency) inhibition returns

quickly and to a large extent. Thus, desynchronization is associated with task performance but resynchronization possibly with the return of top-down control and, thus, the readiness to perform a new task.

### 2.3.2. Tonic alpha power, cognitive performance and inhibition

So far we have focused on findings about short lasting (i.e., phasic) changes in alpha activity that can best be described by ERD/ERS. The extent of ERD, however, does not only depend on task type and stimulation but also on tonic power measured during a reference interval or a (baseline) resting condition (cf. Salenius et al., 1995; Doppelmayr et al., 1998; Klimesch, 1997, 1999 for reviews). We have shown in several studies that large resting or reference alpha power is positively associated with performance (Klimesch et al., 2000; Vogt et al., 1998; Doppelmayr et al., 2002) whereas during actual task performance, small power (large ERD) is related to good performance (e.g., Klimesch et al., 1997b; Doppelmayr et al., 2005). Most interestingly, however, good perception performance (in tasks that require the detection of a visual stimulus under difficult conditions) is related to small alpha power in a reference interval (Ergenoglu et al., 2004) and, thus, to a small ERD or even ERS (Hanslmayr et al., 2005a, cf. Fig. 7). We have interpreted these findings in terms of cortical inhibition and excitation preceding task performance. Perception performance appears to be enhanced if the cortex already is activated (reflected by small reference alpha power, cf. Fig. 7E), whereas memory performance is enhanced if the cortex is deactivated before a task is performed. This interpretation appears plausible if we assume that for visual discrimination a high level of cortical excitation will be helpful to analyze a visual input. For memory performance (and other complex cognitive processes), on the other hand, the initial activation of the cortex may be detrimental because it may interfere with (or even suppress) the high selectivity that is required for accessing a memory trace.

Our findings showing an interaction between pre- and poststimulus alpha are in good line with research on prestimulus alpha power and ERP amplitudes. These studies have demonstrated that ERP amplitudes are correlated with prestimulus alpha activity (e.g., Basar and Stampfer, 1985; Rahn and Basar, 1993a,b; Brandt and Jansen, 1991; Barry et al., 2000).

### 2.3.3. Frontal lobe dysfunction: diminished tonic alpha power and the lack of inhibitory control

More indirect evidence for the inhibition hypothesis comes from research about schizophrenia and frontal lobe dysfunction. It has been shown that the prefrontal cortex plays an important role for the inhibition of irrelevant information and the modulation of the P1-N1 complex in attentional cuing paradigms. Research with schizophrenic patients has shown reliably that (in comparison to normal controls) their resting EEG is characterized by diminished alpha power and augmented theta and delta power (Sponheim et al., 1994, 2000; Miyauchi et al., 1990; Itil et al., 1972, 1974; Iacono, 1982). Most interestingly, Sponheim et al. (2000) have demonstrated that even within a group of schizophrenic patients, diminished alpha power is associated with more negative symptomatol-

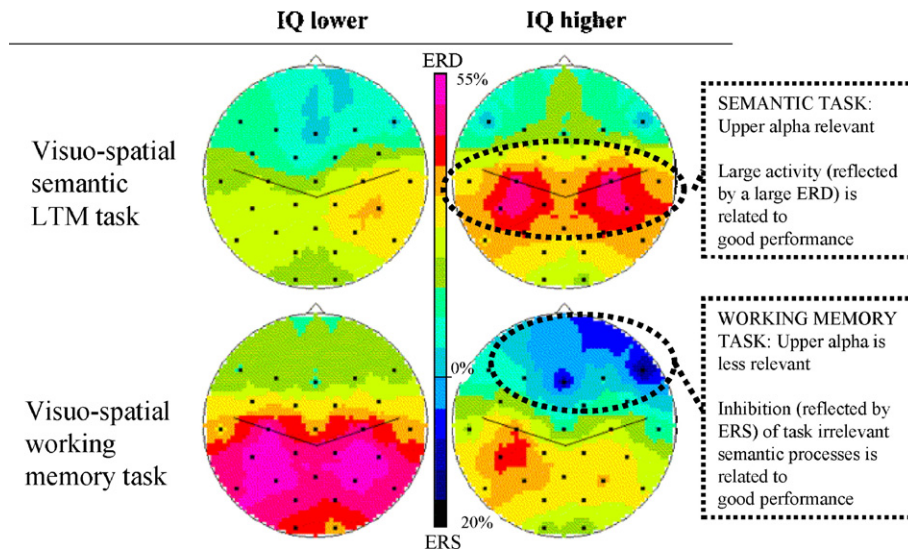
ogy and more deviant brain morphology (e.g., widened third ventricles and enlarged frontal horns of the lateral ventricles). Other studies have shown that the thalamus plays an important role for EEG power abnormalities (e.g., Takeuchi et al., 1994) and that its volume (Gur et al., 1998) and metabolism (Buchsbbaum et al., 1996) is reduced in schizophrenics. Because the third ventricle is bordered on both sides by the medial dorsal thalamic nuclei, the enlargement of the third ventricle (found by Sponheim et al., 2000) may be due (in part) to a reduction in thalamic volume. Thus, diminished alpha power in patients may reflect a dysfunction in thalamic-cortical circuits that is associated with a lack to inhibit irrelevant information (Knight and Grabowecy, 1995)

### 2.4. Intelligence and the inhibition of task-irrelevant brain areas

The findings from our laboratory reported in Section 2.3.2 suggest a positive relationship between ERD and cognitive performance. However, most experiments investigating the neural efficiency hypothesis (originally suggested by Haier et al., 1992 on the basis of a PET study) found the opposite relationship (Neubauer et al., 1995; for similar results see also Grabner et al., 2004; Jaušovec, 1998). We will show in the following that the inhibition hypothesis is capable of resolving this apparent contradiction. An important prerequisite thereby is that in contrast to our studies, those supporting the neural efficiency hypothesis used tasks that do not specifically require semantic memory or long-term memory (LTM) performance.

As an example, the sentence verification task used in Neubauer et al. (1995) requires semantic processing to a minor degree only. Descriptions of artificial spatial relations between symbols used in this type of task have no obvious relationship to information stored in verbal semantic LTM. Thus, the finding of a generally smaller ERD for more intelligent subjects (Neubauer et al., 1995) may indicate their ability to avoid extensive activation of a system that is not directly task-relevant. We have suggested (Doppelmayr et al., 2005) that more intelligent subjects may use only brain areas that are directly relevant (posterior brain regions in this case) and are more efficient in inhibiting brain areas (or distributed processing systems) that are not (or not directly) task-relevant. Because the verbal semantic processing system (associated with frontal brain areas) is not directly relevant for performing the sentence verification task, we would predict these areas to exhibit ERS. Indeed, inspection of the findings of Neubauer et al. (1995) clearly indicate that the smaller ERD at posterior sites which was obtained for more intelligent subjects is accompanied by a larger ERS at frontal sites. Conversely, in a recent study, Doppelmayr et al. (2005) have shown that in a typical verbal semantic task, more intelligent subjects exhibit a significantly larger ERD particularly over the left hemisphere and anterior sites.

To illustrate our hypothesis, let us consider the findings obtained by Grabner et al. (2003) which are shown in Fig. 4. In their study, two different tasks, a visuo-spatial semantic LTM and a working memory (WM) task were used. In the LTM task taxi drivers had to answer questions about which location they would pass when driving from A to B. In this task subjects



**Fig. 4 – Two different processes, focused activation (reflected by ERD), and inhibition of task-irrelevant processes (reflected by ERS) may be related to good performance (reprinted from Grabner et al., 2003, with permission from Elsevier). Two different tasks, a visuo-spatial semantic LTM and a WM task were used. In the LTM task taxi drivers had to answer questions about which location they would pass when driving from panels A to B. In this task subjects solely used their actual knowledge they had acquired driving in this city over several years. In the WM task, the same type of questions were asked by using a fictional map that subjects had to learn before the experiment. The interesting finding is that a widespread ERS can be observed for good performers in the WM task in which LTM processes are less relevant. We speculate that good performers are able to suppress (at least in part) the access to task-irrelevant contents of visuo-spatial LTM and that this suppression is reflected (compared to bad performers) by a generally smaller ERD and increased ERS.**

solely used their actual knowledge they had acquired driving in this city over several years. In the WM task, the same type of questions were asked by using a fictional map that subjects had to learn before the experiment. The interesting finding is that a widespread ERS can be observed for good performers in the WM task in which LTM processes are less relevant. According to our hypothesis, we assume that good performers are able to suppress (at least in part) retrieval of irrelevant contents of visuo-spatial LTM and that this suppression is reflected (compared to bad performers) by a generally smaller ERD and increased ERS. Thus, two different processes, focused activation (reflected by ERD), and inhibition of task-irrelevant information (reflected by ERS) may be related to good performance.

## 2.5. Inhibition and top-down control

In this section, we will argue that synchronized alpha reflects a specific type of inhibition that can best be described in terms of ‘top-down control’. Within Baddeley’s concept of WM (Baddeley, 1992), top-down processes are control functions that can be subsumed under the broad term of central executive processes. We consider a top-down process an attentional control function that keeps processes focused on highly selective aspects of task performance by using inhibition to prevent interference from task-irrelevant brain areas or processing systems.

Let us briefly reconsider three examples, we already have discussed. (i) The increase in alpha activity during retention in memory tasks (cf. Section 3.2.1) can be interpreted in terms of

top-down control on stored information by inhibiting retrieval of interfering information. (ii) ERS in motor tasks may again be interpreted as top-down control on stored motor information to inhibit retrieval of learned responses (e.g., Hummel et al., 2002) or to inhibit access to potentially interfering motor memory traces during imagery (e.g., Neuper et al., 1999). (iii) The general finding that brain areas not involved in the performance of a task exhibit ERS (in motor but also in complex cognitive tasks) can also be interpreted as manifestation of top-down control to keep processing focused on task-relevant areas.

When assuming that top-down control is more relevant in tasks with internal processing demands as compared to the processing of sensory information which primarily is guided by automatic bottom-up processes, alpha power should be larger for the former and smaller during the latter task type. In agreement with this view, Von Stein et al. (2000) found stronger occipital alpha activity in cats during top-down as compared to bottom-up processing. Ray and Cole (1985) and Cooper et al. (2003, 2006) found smaller alpha amplitudes when subjects had to respond to external stimuli as compared to conditions requiring internal mental processing. In a conditioning study, Harris (2005) found that alpha power increased when a stimulus signaled that the unconditioned (visual) stimulus will not be presented in the next trial. Wolfe and Bell (2003) found synchronized alpha activity in a Stroop-like inhibitory control task with children. These findings indicate again that the internal control of attention – particularly under situations when sensory information must not be processed – is associated with an increase in alpha activity.



The importance of internal attentional control also is evident in paradigms investigating mirror neurons. Animal studies revealed that certain cells in area F5 (i.e., the rostral part of the ventral premotor cortex) discharge in response to observed actions (Ferrari et al., 2003). It is believed that mirror neurons represent an observation/execution matching system that is capable of ‘mimicry’. With respect to our hypotheses the interesting prediction is that during the observation of an action – even without concurrent execution – the mu rhythm is expected to desynchronize (over the respective areas of the homunculus) but areas – such as the supplementary motor area (SMA) – that are involved in planning of movements should exhibit increased amplitudes. Indeed, with human subjects observing another person doing a complex motor task, Muthukumaraswamy and Johnson (2004) and Muthukumaraswamy et al. (2004) found ERD over sensory-motor areas but ERS over the SMA. Pineda (2005) concluded that mu activity might reflect the downstream modulation of motor neurons (see also Section 5.4.2).

With respect to memory processes the observation is interesting that ERS can be observed under circumstances where the access to a trace is under top-down control but pronounced ERD is elicited during the actual retrieval of a trace. The following additional and more sophisticated findings support this view.

First, in a ‘selective retrieval’ task, Sauseng et al. (2002, 2005a) found ERS during attempts to access the trace, but ERD when information is actually retrieved (cf. Fig. 5). In this task subjects had to learn verbal labels for each of 8 abstract visual patterns. Then the verbal labels were presented and subjects had to retrieve the respective pattern (cf. Fig. 5A). The results show that during retrieval attempts evoked theta oscillations spread from anterior to posterior recording sites (Fig. 5B). When information actually is retrieved, the direction reverses and theta spreads to frontal sites. This time point – when direction reverses – varies between subjects to a large extent (at around 800 ms) but is significantly correlated with subsequent retrieval performance. Most importantly, up to this time point ERS can be observed but ERD with the onset of retrieval (Fig. 5C).

Second, in a WM task, Sauseng et al. (2005b) found upper alpha ERS when subjects had to manipulate information during a retention interval. Two conditions were compared. Subjects had either to remember visuo-spatial information (control condition) or to manipulate it (‘top-down’ condition; cf. Fig. 6A). In each trial a 4×4 matrix containing 3 targets (colored squares) was presented for 500 ms. If the three targets were green, their positions had to be kept in memory for 2500 ms and had to be compared to three gray labeled matrix positions of a probe, presented for 1000 ms. Subjects had to indicate by a button press whether the target positions were the same. If the color of the targets was red, their positions had to be mirrored around a vertical line in the matrix and then retained in memory for 2500 ms. As in the first condition, the target positions had to be compared with the probe item. The largest differences between the two conditions were found for the first half of the retention interval. During manipulation upper alpha ERS at frontal sites and ERD at posterior sites was larger than during pure retention (cf. Fig. 6B). Absolute alpha power, however, showed that during manipulation brain activation reflects a state of “alpha equilibrium”—where

alpha power exhibits a topographically flat distribution (cf. Fig. 6D). Most interestingly, this effect was not only found with alpha power but also with alpha frequency. As shown in Fig. 6D, alpha frequency at frontal sites increased to values similar to those at occipital sites during manipulation. In contrast, during pure retention occipital alpha was clearly faster than prefrontal alpha. For this time window of alpha equilibrium, the calculation of cross-correlations and coherence revealed increased long-range integration between anterior and posterior sites. Thus, it appears that a state of alpha equilibrium enhances or enables cortico-cortical communication. Because during manipulation frontal sites are leading and posterior sites trailing (Fig. 6C), we conclude that anterior sites control in a top-down manner mental operations on the memory trace stored at posterior sites. Because in addition to manipulation, the rearranged information had also to be visually imagined, we expect increased activation over posterior cortical areas (as, e.g., demonstrated by Kosslyn et al., 1999) as compared to pure retention. This process is reflected by a stronger upper alpha ERD over posterior areas (for similar results cf. Tesche et al., 1995).

Top-down processing not only is characterized by changes in alpha amplitude. There is growing evidence that phase or latency shifts between higher and lower hierarchical cortical areas in the alpha frequency might indicate top-down activation. Evidence for this view is discussed in relation to the timing aspect in Section 4.2.

## 2.6. Indirect evidence for alpha reflecting different states of brain activation

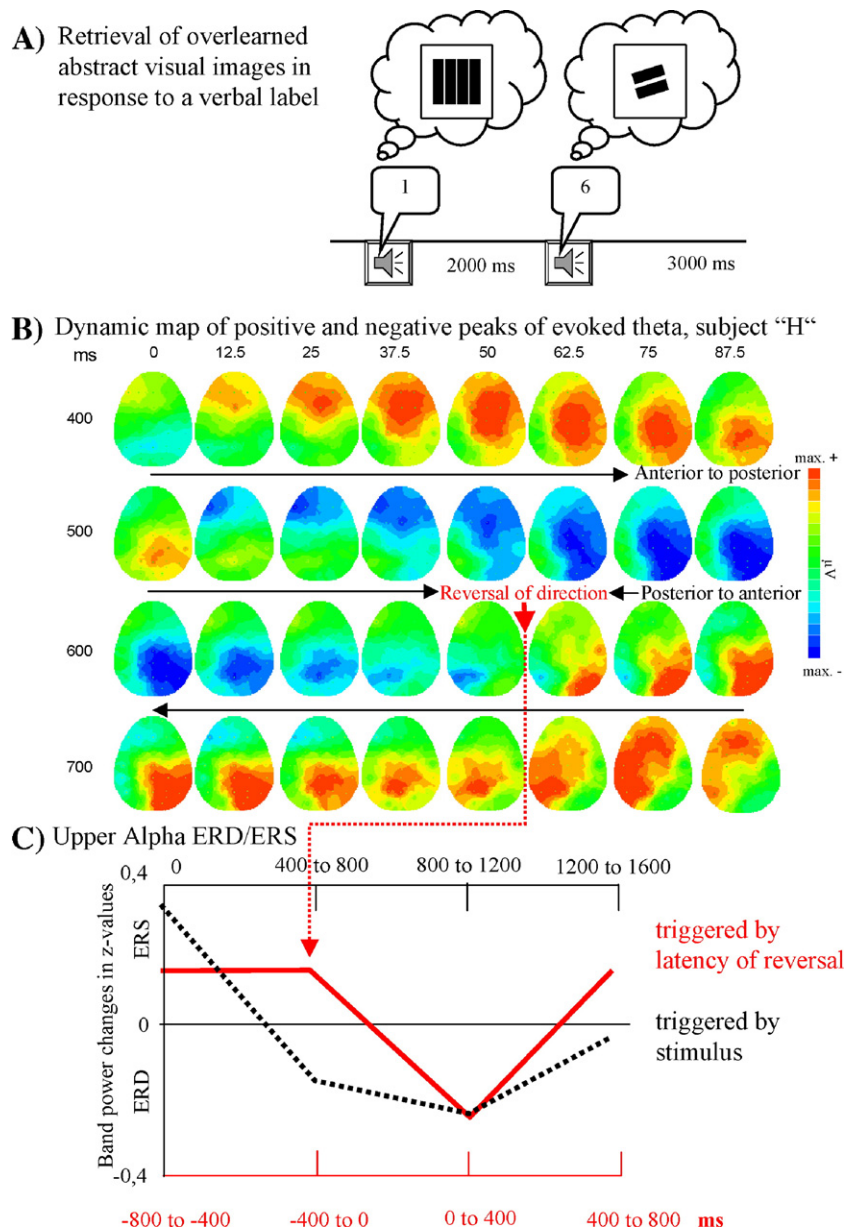
Besides the direct investigation and experimental manipulation of spontaneous alpha activity there are at least two other lines of research that are relevant for the evaluation of our hypotheses. One is related to the investigation of driven alpha activity and the other to the investigation of the relationship between alpha and brain metabolism.

### 2.6.1. Driven alpha activity, ERD and ERS

It is an interesting fact that driven alpha activity shows a very similar functional relationship as we have found for ERD and ERS. Driven activity is observed if a sensory stimulus is presented repetitively and at a frequency that prevents the EP from returning to baseline (this frequency is at about 2.5 Hz and higher; e.g., Ding et al., 2006). The response elicited in the EEG is called driven rhythmic activity or steady-state evoked potential (SSEP). Although SSEPs can be observed also with auditory stimulation, the best investigated case is the steady-state visually evoked potential (SSVEP).

In using the steady-state probe topography (SSPT) technique, Silberstein and his colleagues were able to demonstrate that amplitudes of the SSVEP generally tend to decrease in a very similar way as alpha does (e.g., Silberstein et al., 1990, cf. Silberstein, 1995 for a review). More recently, Silberstein et al. (2001) reported SSVEP amplitude increases that are associated with the retention of items in WM. This again mimics the spontaneous alpha response, in this case ERS, which was observed consistently during the retention of information held transiently in memory. The SSVEP method also proved useful to detect load-dependent increases in coherence



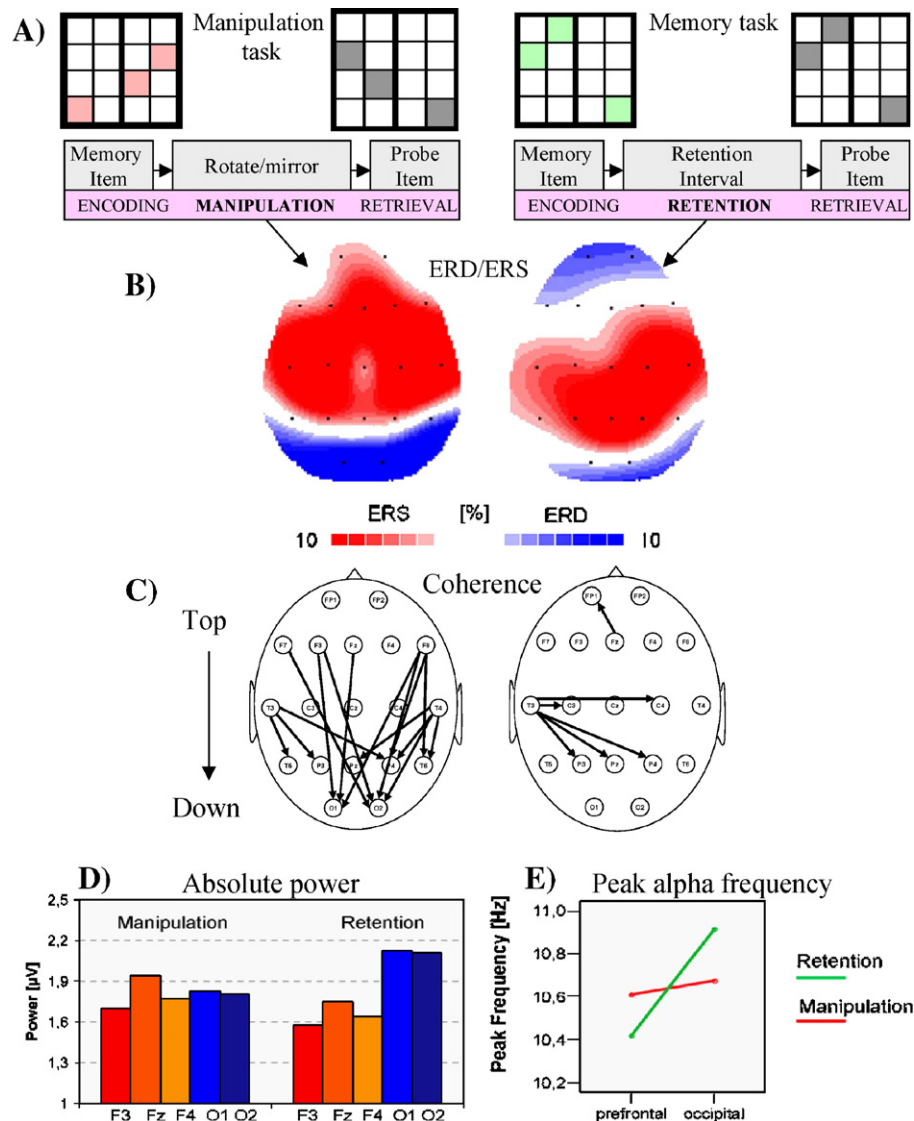


**Fig. 5** – In a ‘selective retrieval’ task, [Sauseng et al. \(2002\)](#) found evidence for the hypothesis that upper alpha starts to desynchronize when a subject actually starts to access a stored memory trace. (A) Subjects had to learn verbal labels for each of 8 abstract visual patterns. Then the verbal labels were presented and subjects had to retrieve the respective pattern. (B) During retrieval attempts evoked theta oscillations spread from anterior to posterior recording sites. When information actually is retrieved, the direction reverses and theta spreads to frontal sites. This time point – when direction reverses – varies between subjects to a large extent (at around 800 ms) but is significantly correlated with subsequent retrieval performance. (C) Most importantly, up to this time point ERS can be observed but ERD with the onset of retrieval (reprinted from [Sauseng et al., 2002](#), with permission from Elsevier ).

between cortical regions ([Silberstein et al., 2003](#)). The findings from the research group of Silberstein are particularly interesting because they use a flicker with a frequency in the upper alpha range (of 12 or 13 Hz) and because their findings are completely in line with the behavior of ‘natural’ alpha.

Other studies, however, apparently contradict this notion because increases and decreases in SSVEP power in the alpha range were found together (e.g., [Morgan et al., 1996](#); [Chen et al., 2003](#); [Ding et al., 2006](#)). But unlike Silberstein and colleagues

who used a Ganzfeld flicker, in the latter studies, the flicker appeared only in part of the stimulus display and was associated with the relevant or irrelevant stimulus. Thus, experimental variations in flicker presentation may be confounded, e.g., with task difficulty. Task difficulty will change alpha power and, as a consequence, the resonance properties of the flicker (SSVEP amplitude depends largely not only on individual alpha frequency but also on power as was shown, e.g., by [Sakamoto et al., 1993](#)). As an example [Ding et al. \(2006\)](#)



**Fig. 6 – Access to a stored memory trace is associated with traveling alpha waves probably reflecting top-down processes (Sauseng et al., 2005b; permission for reproduction currently requested).** (A) The memory task consisted of two conditions. Subjects had either to remember visuo-spatial information (control condition) or to manipulate it ('top-down' condition). In each trial a 4×4 matrix containing 3 targets (colored squares) was presented. If the targets were green, their positions had to be kept in memory and had later to be compared to three gray labeled matrix positions of a probe. If the color was red, the positions had to be rotated around a vertical line in the matrix and then retained in memory. The data show the first half of the manipulation or retention interval. (B) During manipulation upper alpha ERS at frontal sites and ERD at posterior sites was larger than during pure retention. (C) During manipulation and retention the topographic pattern of coherence is strikingly different. As determined by cross-correlations, latency shifts showed a top-down pattern of activation in the manipulation task that is characterized by leading frontal and trailing posterior sites. (D) During manipulation absolute alpha power and (E) alpha frequency showed a state of "alpha equilibrium". Alpha power and frequency increased at frontal sites to values similar to those at occipital sites. It appears as if a state of alpha equilibrium enhances or enables cortico-cortical communication (reprinted from Sauseng et al., 2005b, with permission from Wiley).

found an increase in the upper but decrease in the lower alpha band when subjects attended to the flicker and at the same time ignored a random broadband flicker. In the opposite condition, when subjects had to attend the broadband flicker, power in the upper alpha band decreased, but power in the lower band increased. But these two conditions are not directly comparable because task difficulty was different in

the two conditions. Targets were presented more frequently during the flicker – as compared to the random broadband flicker – condition (the hit rate for a 10 Hz flicker was between about 0.6 to 0.7 but around 0.9 for the broadband flicker). Consequently, as Ding et al. (2006) reported, 'normal' alpha power (i.e., power after the flicker frequency and its harmonics were removed) became suppressed during the more difficult

flicker condition in the alpha frequency range. Thus, the influence of task difficulty and alpha suppression might very well be responsible for these divergent findings because it is known that the extent of alpha power has a strong influence on the SSVEP amplitude. Nonetheless, it should be mentioned that an increase in the SSVEP alpha amplitude for an attended stimulus or hemifield (e.g., Morgan et al., 1996) is well in line with our hypothesis. Focused attention clearly establishes a top-down process and probably increases the responsiveness of those neural networks that already 'operate' in alpha. It should also be noted that increases in SSVEP power were also found in other frequencies (e.g., Hillyard et al., 1997; Müller et al., 2003; Ding et al., 2006). The behavior of different frequencies may very well be inter-related but their possible interaction is not yet understood.

### 2.6.2. Alpha and metabolic rate

According to the inhibition hypothesis, we expect a negative correlation between metabolic rate and alpha power. Although active inhibitory neurons would also increase the metabolic rate, their percentage in the cortex appears too small to exert a strong influence. In the cortex 85% of all neurons are excitatory and only 15% inhibitory (Braitenberg and Schüz, 1991). In other brain areas, particularly in the thalamus, inhibitory neurons are much more abundant.

Several studies relating metabolic activity to alpha power do show a negative correlation indicating that a decrease in alpha is related to an increase in cortical metabolic rate. Goldman et al. (2002) were the first, who have shown a reliable negative correlation. Laufs et al. (2003a,b) and Moosmann et al. (2003), using new technology allowing for a simultaneous and continuous recording of fMRI and EEG, report large negative correlations between alpha power (at 8–12 Hz, recorded from O1 and O2) and the fMRI-blood oxygen level-dependent (BOLD) signal in cortical areas. Topographical differences are remarkable. Whereas Laufs et al. (2003a,b) observed negative correlations in a widespread frontal-parietal network, Moosmann et al. (2003) found the most consistent negative correlations for occipital regions (Brodmann 18 and 19). In some areas, however, positive correlations were also obtained. Laufs et al. (2003a,b) report positive correlations for occipital and mid-cingulate regions. Moosmann et al. (2003) obtained a weak positive correlation for the thalamus. With respect to the thalamus, similar results were reported by Sadato et al. (1998) using PET and by Goldman et al. (2002) using an interleaved EEG-fMRI recording approach. Although these findings seem to support the thalamic pacemaker role, they must be interpreted with caution because areas (like the thalamus) that are close to ventricles and/or large vessels are prone to reflect fMRI artifacts (for a discussion, see Moosmann et al., 2003).

Contrary to these results, however, Lindgren et al. (1999) obtained a negative correlation between alpha and metabolic activity in the thalamus. The latter finding is based on recordings during a resting situation with alternating periods of open and closed eyes. Thus, the negative correlation may simply be due to the influence of light stimulation rather than a direct relationship between metabolic rate and alpha power. Light stimulation (during eyes open) leads to an increase in thalamic activity but to a decrease in alpha. Conversely, no stimulation (during closed eyes) leads to decreased thalamic

activation but increase in alpha. This methodological problem was avoided by Laufs et al. (2003a,b) and Moosmann et al. (2003) who used a continuous resting task with closed eyes. Thus, their data reflect a direct association between spontaneous fluctuations in alpha and brain metabolism (independent of the influence of stimulation). In a separate task, Moosmann et al. (2003) used near infrared spectroscopy to demonstrate that alpha suppression per se (during open eyes in a completely dark room) and not light stimulation is directly related to an increase in brain metabolism.

There are also studies reporting a consistent positive correlation between relative alpha power and metabolic rate. As an example, Schreckenberger et al. (2004) used PET with concurrent EEG recordings and found that the PET signal was increased during periods of pronounced alpha activity. The reasons for these conflicting results are not clear. The use of relative alpha power (related to total power) may play an important role. The subjects of Schreckenberger et al. (2004) were asked to relax with eyes closed in a quiet and darkened room. Thus, if subjects became drowsy (in contrast to fMRI which emits loud noise, PET is quiet), periods of increased delta and theta activity will lead to a decrease in relative alpha power, whereas periods with a lack of large delta and theta will increase relative alpha power. Thus, even in a case absolute alpha would remain stable over the entire recording session, power changes in lower frequencies may be responsible for the observed positive relationship between relative alpha power and metabolic rate.

In general, it should be noted that the interpretation of correlations between alpha and metabolic rate is problematic. Synchrony and firing rate may be important factors influencing the type of observed relationship. Large alpha amplitudes may stem from high synchrony between only a few percent of neurons with the majority of neurons being relatively inactive and exhibiting only a low firing rate thereby producing minimal metabolic activity (Nunez and Silberstein, 2000). On the other hand, decreasing synchrony but increasing EPSP amplitudes (leading to increased firing rate) in a larger number of neurons may produce small EEG amplitudes and a large metabolic signal.

## 3. The timing aspect

As discussed in Section 2, an increase in rhythmic activity results in two different effects, in a general decrease in firing rate and an increase in rhythmic discharges (cf. Figs. 1A with B). We assume that the first effect reflects inhibition as discussed in Section 3. The second effect, however, underlies the timing of neuronal activity and will be discussed in this section.

The crucial aspect – as outlined in Fig. 1 – is that an increase in inhibition (driving an oscillation) is accompanied by an increase in oscillatory activity that results in a stricter timing of neural activity. In this sense, oscillations are an extremely useful mechanism to control the time window in which neurons are most likely to fire. One important aspect thereby is that in a complex network, common target cells will tend to receive neural activity synchronously. This increases the likelihood that these cells will be activated selectively and that one brain region might influence another. The importance



of this and additional aspects for neuronal communication was outlined in several comprehensive reviews (cf., e.g., Varela et al., 2001; Fries, 2005).

It is important to emphasize that this influence from inhibition driving an oscillation is different from inhibition changing the excitation level of principal cells in a tonic way (cf. the two different scales of the left and right side of the respective diagrams in Fig. 1). A tonic change in the excitation level of principal cells (towards increasing inhibition) would never facilitate the timing of neural activity but would eventually result in silencing all cells and in a complete blocking of information processing. In contrast, inhibition due to oscillatory activity may allow selective information processing at least within a certain range of increased oscillatory activity. Nonetheless, it is very well conceivable that beyond a certain magnitude of increased oscillatory activity, most or all principal cells might become silenced as well.

### 3.1. Ongoing alpha and the timing of cortical processes

The EEG reflects changes in postsynaptic (i.e., dendritic) membrane potentials (cf. Logothetis et al., 2001) primarily in cortical neurons. Thus, rhythmic changes in the EEG, typically observed during pronounced alpha activity, reflect rhythmic changes in the excitability of (primarily cortical) neurons. Rhythmic activity must have a strong influence on information processing in the brain, because the generation of action potentials is much more likely during the excitatory (extracellular negative) phase than during the less excitatory or inhibitory (extracellular positive) phase of an oscillation.

It has been suggested for a long time that the cortex exhibits cyclic changes between maximal and minimal responsiveness (Bishop, 1933) that are related to the negative and positive phase of alpha. Several early studies were indeed able to show that reaction time (RT) and other behavioral measures depend on the alpha phase during stimulation. As an example, Varela et al. (1981) asked their subjects to judge whether two briefly exposed visual stimuli with asynchronous onset appear as simultaneous or moving stimuli. They found that stimuli presented during negative polarity were perceived simultaneous whereas those presented during positive polarity appeared moving. Dustman and Beck (1965) found that RT to the onset of a light flash was fastest during the surface positive alpha cycle. In assuming that a visual stimulus is processed in the cortex after a delay (due to peripheral transmission time) of about 50 ms, the critical time window for the prediction of behavioral effects is not the phase of alpha at stimulation but at the time of cortical processing which is 50 ms poststimulus for the present example. Thus, if a stimulus is presented during the positive cycle, alpha will be at its negative cycle 50 ms later (in assuming that alpha period is about 100 ms). In assuming that alpha is now in its excitatory phase, stimulus processing in the visual cortex will be enhanced and RTs will decrease. When applying the same reasoning to the findings of Varela et al. (1981), we conclude that stimuli presented during the positive cycle should coincide with enhanced stimulus processing in the brain which in this case means that the two stimuli would not be perceived as one simultaneous but instead as two separate (moving) stimuli. Thus, there are reasons to assume that alpha

phase controls cortical excitability. A variety of other studies have documented that alpha phase is related to different behavioral measures (e.g., Nunn and Osselson, 1974; Rice and Hagstrom, 1989; Callaway and Yeager, 1960).

### 3.2. Traveling alpha waves and top-down processes

Topographical analysis of the phase of ongoing oscillations between recording sites has led to the detection of 'traveling' waves (best documented for alpha) moving in a task-dependent manner, e.g., from anterior to posterior sites (e.g., Sauseng et al., 2005b; for a review cf. Nunez et al., 2001; Silberstein, 1995). The fact that 'travel' speed is in the range of neural transmission (e.g., Schack et al., 2003) suggests that spreading direction of alpha reflects some sort of communication between brain areas.

In an elegantly designed animal study, Von Stein et al. (2000) have demonstrated that traveling alpha waves may reflect a spread of cortical activation in the sense that one brain region controls – in a top-down manner – activation in another region. The EEG was recorded from cats using electrode arrays implanted in three cortical areas (areas 17, 7 and 5). The animals were trained to attend to visual stimuli displayed on a monitor. The experimenter observed the animal and a trial was started only if the cat attended the display. A trial consisted of a neutral mask (the preparatory stimulus) moving slowly across the screen. The cat was trained to track the mask until – after a random interval – a second stimulus (drawing of a mouse or rectangle) appeared. Balanced between animals, either the mouse or the rectangle was assigned the 'go' or 'no-go' stimulus. When the 'go' stimulus appeared, animals had to press a lever, when the 'no-go' stimulus appeared they had to continue tracking. They were rewarded for correct performance under both conditions. This is an important detail of the design because it guarantees that the animals remain fully attentive throughout the trial. After extensive training, novel stimuli (stimuli with which the cat was not confronted during training) were presented randomly interspersed in the sequence of learned stimuli. Because there was no particular response required, animals were rewarded either for pressing the lever or for continuing tracking. The main results are that significant cross-correlations in the alpha frequency range could be observed between areas 17 (primary visual cortex) and 7 (visual association cortex) but only for expected stimuli (mouse or rectangle) and not for novel, untrained stimuli. In contrast, both types of stimuli have led to significant cross-correlations in the gamma frequency range. Most interestingly, by considering the direction of the phase lag, it could be demonstrated that area 7 is 'leading' and, thus, drives area 17 whereas the opposite direction of phase lag (although quantitatively much smaller) was observed for the gamma band. These findings nicely demonstrate that only the processing of 'familiar' stimuli – for which a memory trace was established during the training session – is associated with a top-down directed interaction (between the association and primary sensory area) that showed up only in the alpha band. On the other hand, sensory processes (which are necessary for both, expected and novel stimuli) are associated with a bottom-up activation reflected by gamma activity. These findings support

the hypothesis that alpha is related to the semantic encoding of familiar stimuli and suggest a top-down process in the sense that a learned memory trace is used for the encoding of an expected stimulus.

The conclusions from this meanwhile classical work of Von Stein et al. (2000) are supported by the findings from Sauseng et al. (2005b) who analyzed upper alpha oscillations and found that during top-down processing in a visuo-spatial task frontal areas are leading and posterior sites are trailing (cf. Fig. 6C). In a WM task, Halgren et al. (2002) observed an alternation of phase shifts from visual association cortex to parietal and central structures and propagation back to the occipital cortex in a broad frequency range from 4 to 12 Hz. This finding was interpreted as rapid change between bottom-up and top-down processing. In general, we assume that traveling alpha reflects waves of spreading activation moving from one area to another.

### 3.3. Alpha phase reset: an event-related mechanism to control top-down processing?

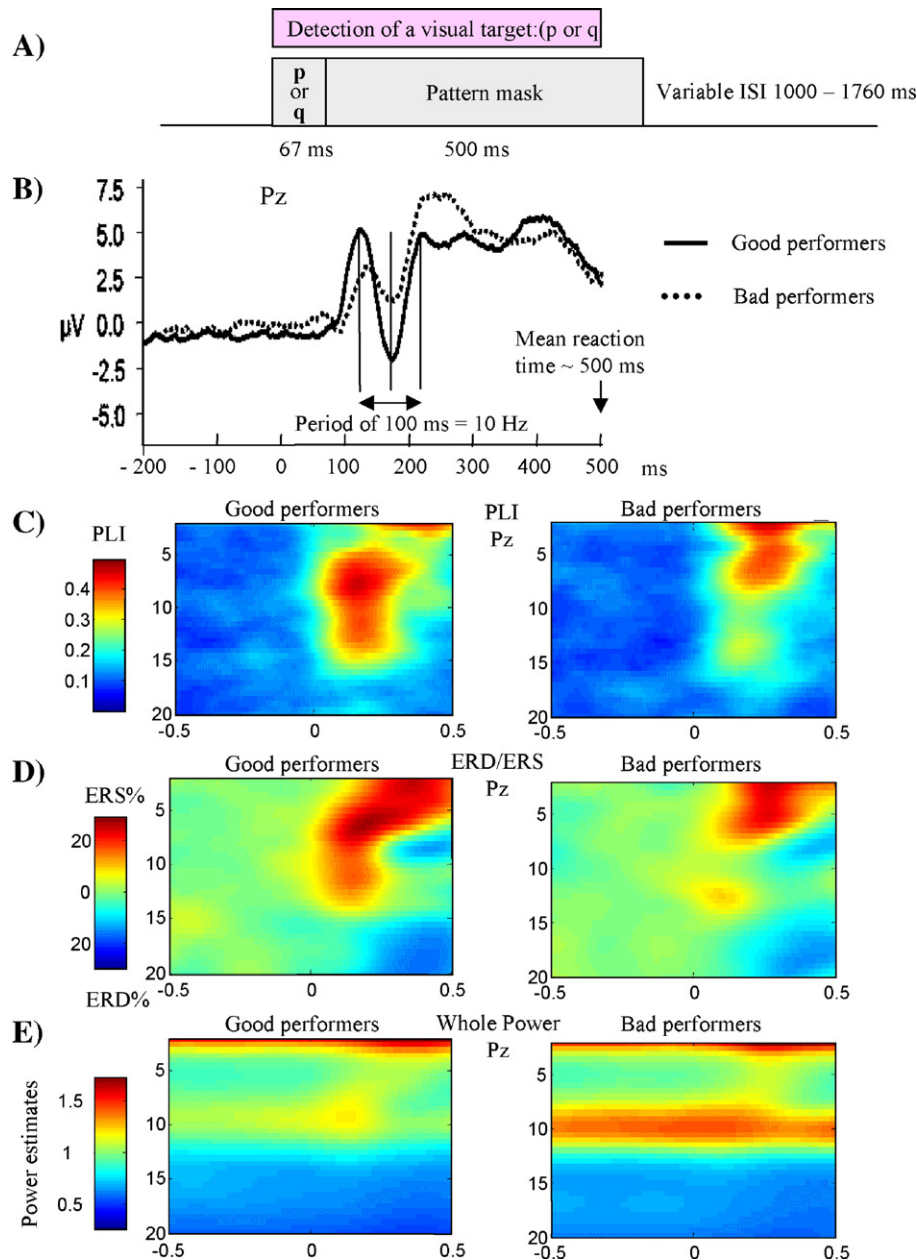
Evidence reviewed in the two preceding sections strongly suggests that ongoing alpha phase controls cortical activation. The interesting point is that accepting this notion – which means that alpha is capable of controlling the timing of cortical activation in the range of milliseconds – inevitably has direct consequences for the interpretation of the event-related alpha response. In event-related designs, the presentation of a stimulus is the natural starting point for a cascade of different processes that require exact timing and coordination. If we assume that alpha plays a similar role in event-related processes, the logical consequence is that the phase of alpha must be reset at some point of time poststimulus. But when does the reset occur and to which value is phase being reset?

We proceed from the general assumption that early processing of a stimulus is accompanied by expectancy and, thus, is ‘embedded’ in a top-down process. We also assume that the P1 is the earliest manifestation of a top-down process during early sensory processing. The general idea is that under conditions where sensory processing is guided by a specific expectancy, e.g., about the spatial location and/or type of stimulus, the P1 amplitude will be larger than under conditions where specific expectancies are lacking. Empirical evidence for this view comes from studies investigating the influence of attention, directed to a specific location in a visual array. As an example, if a cue indicates that a target will appear in the left hemifield, the P1 is significantly larger over contralateral as compared to ipsilateral recording sites (e.g., Mangun and Hillyard, 1991; Gazzaniga et al., 2002 for a review). Most interestingly, recent research has shown in addition that the P1 also is sensitive to non-spatial attention. Using a search paradigm with stimulus arrays containing 8 rectangles, Taylor and Khan (2000) found that in the color/form pop-out search the same color stimulus elicited a significantly shorter P1 latency when used as target (in the color pop-out search) as compared to the form pop-out search when this stimulus was used as non-target. This finding clearly suggests that the P1 is modified by object-specific top-down attentional processes. But the P1 component also is sensitive to sensory-semantic information. As an example, when subjects were presented a series of briefly exposed pictures of natural scenes and asked

to judge whether they contained an animal, a slightly but consistently larger P1 was observed for targets (pictures containing an animal) than for non-targets (Taylor, 2002). Taylor et al. (2001) used facial and control stimuli (unknown upright and inverted faces, scrambled faces, eyes-only, flowers and checkerboard targets). As expected, they found that the N170 is most sensitive to faces. Most interestingly, however, already the P1 exhibited shorter latencies to upright faces than inverted faces and control stimuli. Thus, whereas the N170 is associated with the identification of a face, the P1 may be associated with more global processes, probably the categorization of the presented stimuli in faces versus non-faces. Taken together, these findings support the view that the P1 reflects the early influence of top-down processes on sensory-semantic processing.

With respect to the timing aspect of our hypothesis, the critical assumption is that the P1 is generated (at least in part) by a phase reset of alpha and that the surface positivity of this component represents the deactivating/inhibitory phase of alpha. This latter assumption is based on the basic mechanisms of oscillations that are well documented for theta: The deactivating/inhibitory phase operates as inhibitory filter to achieve a high signal to noise ratio by allowing only a small number of cells to process information selectively and silencing the majority of other cells. With respect to hippocampal theta oscillations, there is indeed evidence that most hippocampal GABAergic cells oscillate in theta, whereas only a small minority of pyramidal cells do so (Fox and Ranck, 1981; Freund and Antal, 1988; Stewart and Fox, 1990; Traub et al., 1989; Mehta et al., 2002). We assume that in the time window of the P1 early semantic classification/identification processes are initiated. Furthermore, we assume that this time window is the earliest where top-down processing can interact with bottom-up processing. Early sensory-semantic information processing which is enabled by excitatory processes meets an inhibitory filter at around the time window of the P1 (around about 100 ms) when early semantic encoding processes are shaped by top-down processes.

Results reported by Hanslmayr et al. (2005a) demonstrate nicely that the P1 reflects the timing of early categorization processes and that the amplitude of the P1 most likely is generated (at least in part) by a reset of alpha. In this study briefly exposed letters (p’s and q’s, presented in random sequence) followed by a pattern mask were presented and subjects had to detect either the letter ‘p’ or ‘q’ (cf. Fig. 7A). ERPs were characterized by a prominent P1-N1 complex that exhibits pronounced evoked alpha activity (cf. Fig. 7B). Most interestingly, compared to bad performers, good performers showed a larger P1-N1 complex that was associated with a significantly larger alpha phase locking index (PLI). These findings indicate that good (target categorization/identification) performance is reflected by increased alpha phase locking. They imply that increased alpha PLI, responsible in part for the amplitude increase of the P1-N1 complex, reflects an exact timing of early categorization/identification processes that is essential for good performance (cf. Klimesch et al., 2004 for similar findings in a picture recognition task). It is worth mentioning that event-related power changes in the upper alpha frequency range were characterized by ERS rather than ERD (cf. Fig. 7D). According to our hypothesis increased evoked



**Fig. 7** – In a visual target detection task in which subjects had to identify briefly exposed letters (A), the event-related alpha response is primarily characterized by phase locking and not by power changes (reprinted from [Hanslmayr et al., 2005a](#), with permission from Elsevier). (B) The waveform of ERPs is characterized by evoked alpha activity, which is more pronounced for good performers. (C) The extent of alpha phase reset, as measured by the phase locking index (PLI) is larger for good than bad performers. (D) The event-related change in upper alpha is characterized by ERS and a complete lack of ERD. (E) The lack of desynchronization and the large differences in prestimulus power between good and bad performers is clearly evident in the time/frequency/(wavelet) power plot.

alpha (as reflected by a large P1) but a lack of ERD suggests increased top-down control during access of a trace without retrieval. This interpretation is quite plausible, because subjects knew that only one of two letters can appear. Thus, the traces of the two letters may have been already preactivated before the letters were presented and the task-relevant process just is to provide fast access to the relevant trace.

Consistent with the view that the P1 is generated (at least in part) by a phase reset of alpha oscillations are findings

showing that the latency of the P1 varies as a function of individual alpha frequency (IAF) in a sense that short latencies are associated with high IAF; cf. [Klimesch et al., 2004](#)) and that the P1 is generated by phase alignment of different frequencies primarily in the alpha range ([Gruber et al., 2005](#)).

It should be noted that the issue of phase reset is highly controversial primarily because evidence for phase concentration (cf. [Makeig et al., 2002, 2004](#); [Klimesch et al., 2004](#)) may be due to an evoked component that is superimposed on



ongoing oscillations. When calculating phase (for an oscillation with a certain frequency), the EEG data must be filtered. But by filtering a transient evoked response would be turned into a transient change in the phase of an ongoing oscillation (Mäkinen et al., 2005). Consequently, phase concentration does not provide unambiguous evidence for phase reset. Nonetheless, when considering phase reset as a general mechanism for the generation of (early) ERP components (as was suggested by Basar and colleagues for a long time; e.g., Basar, 1999), several predictions can be made that all have been confirmed empirically: (i) phase concentration is expected during the time window of the P1-N1 complex (e.g., Makeig et al., 2002; Klimesch et al., 2004; Brandt, 1997; Barry et al., 2004; Jansen et al., 2003), (ii) phase concentration takes place at least in that frequency range that is evident as a dominant ongoing oscillation already during a prestimulus interval (Makeig et al., 2002; Klimesch et al., 2004), (iii) the frequency characteristics of evoked activity (i.e., early ERP components) resemble those of the ongoing oscillations (Klimesch et al., 2004). (iv) As compared to the prestimulus period, oscillatory power must not increase during the event-related response (Klimesch et al., 2004; Shah et al., 2004). In addition, simulation studies revealed that the event-related EEG response cannot solely be explained by the sum of the evoked response and the 'background' EEG. At least to some (but significant) extent the event-related EEG response is non-additive and can be best explained by phase reset (David et al., 2005; Hanslmayr et al., *in press*).

An important point is the assumption that alpha phase reset (generating the P1 at least to some extent) takes place at around 100 ms (for visual stimuli). A comparatively late phase reset is consistent with the reviewed findings about the influence of phase on behavioral measures. The earlier the reset would take place, the less influence it would have on information processing. As an example, if alpha would be reset to the positive peak already at around 25 ms, the ongoing phase could never exert a strong effect (on behavioral measures or cortical processing) when assuming that sensory processing in the cortex starts later, at around 30 or 50 ms in the auditory and visual cortex respectively. Furthermore, when assuming a reset to the positive peak already at around 25 ms we would have to expect a very early evoked component with positive polarity and a frequency characteristic in the alpha range. Very early visual components, such as the C1, however, have several properties that are clearly distinct from the P1 (cf. Di Russo et al., 2002).

In conclusion, we assume that during phase reset cortical excitability is reorganized in a way that those brain areas that are task-relevant are set in a comparatively less excitatory or inhibitory state at exactly that time window when bottom-up sensory processing interacts with top-down processes. Alpha phase reset may, thus, be understood as an early inhibitory filter that enables the emergence of a highly selective and excitatory encoding network. Consistent with this view are also findings about cross-modality experiments. Basar-Eroglu et al. (1991); Basar et al. (1991) have demonstrated that early evoked alpha can be observed primarily with visual stimulation in the visual (but not auditory) cortex and – vice versa – primarily with auditory stimulation in the auditory (but not visual) cortex (for a review cf. Schürmann et al., 1997).

### 3.4. Event-related alpha synchronization between brain areas

Information processing is a highly distributed process, and as a consequence of our conclusions outlined in the previous section, we have to assume that during and after phase reset a dynamic, topographic pattern of alpha synchronization (measured in terms of coherence or phase synchronization) will be observed between different brain areas involved in the processing of the stimulus and/or task (Varela et al., 2001).

There is evidence for this view. As an example, Mima et al. (2001) investigated the question, whether an event-related increase in inter-hemispheric coherence (in a broad range of 2–40 Hz) can be observed during object recognition. The results showed a brief, highly significant increase in inter-hemispheric coherence (particularly at occipitotemporal sites) that was restricted to the alpha band (8–10 Hz) and to a time window of 117–373 ms. Most interestingly, this synchronization pattern did not exhibit a significant phase lag and occurred *before* a (significant) decrease in alpha power developed at these sites. It could be observed only during recognition of familiar objects (spanning the midline) but not for meaningless objects or passive viewing conditions. When presented laterally, familiar objects did not induce increased interhemispheric coherence. Thus, an increase in alpha coherence appears to be selectively related to inter-areal alpha synchronization between those (interhemispheric) scalp regions that are related – most likely – to the early semantic encoding of objects. With respect to our hypothesis, the general idea is that during and immediately after the time window of the P1, alpha is relevant for the timing of early semantic encoding which is reflected by a topographic synchronization pattern between relevant brain areas. It is important to emphasize that alpha synchronization takes place before a task-related increase in cortical activation (reflected by alpha suppression) can be observed.

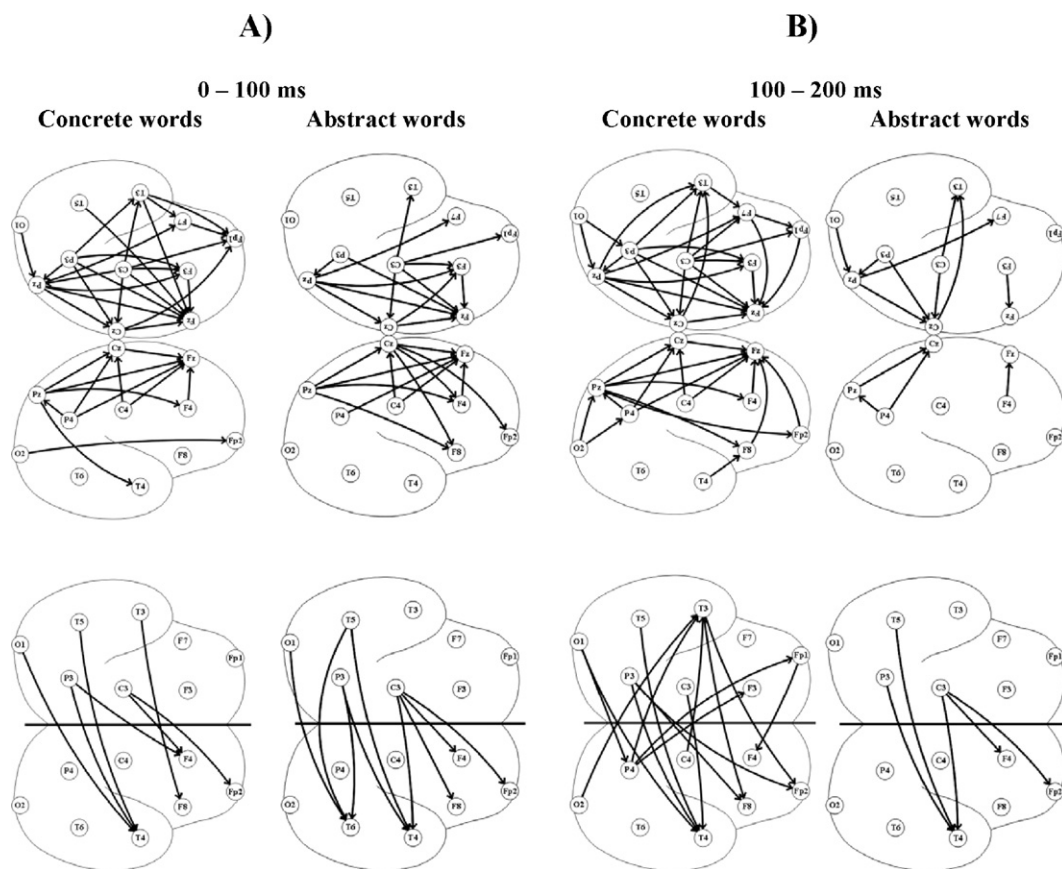
In using depth electrodes, Klopp et al. (2000) investigated coherence changes between the fusiform gyrus (as target area) and 15 other sites. The rationale of this study is based on the fact that the fusiform gyrus (lying anterior to the retinotopic visual areas but posterior to memory-relevant regions of the ventral temporal lobe) becomes specifically activated by faces with a peak at about 180 ms after stimulus onset (as determined by MEG and intracranial EEG studies; cf. Halgren et al., 2000; Allison et al., 1994). The results show a sharp, transient increase in coherence between the fusiform gyrus and all other sites around 160–230 ms poststimulus but only when subjects performed a face, not a word recognition memory task. This coherence increase was largest in the alpha band (around 10 Hz) and second largest in gamma. During maximal coherence (at about 200 ms) a transient (alpha and gamma) phase locking between the fusiform gyrus (as target region) and all other sites was observed. Analysis of phase lag (for alpha and gamma within the time window of maximal coherence) revealed that lag values were directly related to the distance from the fusiform gyrus (with frontal areas exhibiting the largest and lingual and parahippocampal sites the smallest values). Considering the time window of these findings which coincides with the peak amplitude of the N1 for face recognition reported in other studies, the simultaneous

increase in alpha and gamma coherence appear to be related to the semantic identification of faces. The transient phase locking with other sites and the increase in lag with distance suggests a bottom-up information transmission during semantic encoding. With respect to our hypothesis, the interpretation is that during the P1 time window semantic encoding is initiated but semantic identification occurs later, probably during the N1 time window. The bottom-up directed phase lag may reflect the lack of specific expectancies which is due to the type of task. The fact that in contrast to Klopp et al. (2000), Mima et al. (2001) reported a zero phase lag synchronization pattern could be due to differences in recording and analyzing methods. In contrast to Klopp et al. (2000) using intracranial recordings, coherence between scalp electrodes was analyzed by Mima et al. (2001). As coherence on the scalp level may be influenced by volume conduction and by the kind of reference used, this might explain the disaccoring results of Klopp et al. (2000) and Mima et al. (2001).

Schack et al. (2003) investigated alpha phase synchronization during the encoding of spoken words that subjects were instructed to remember. Four lists containing either 25 concrete or 25 abstract nouns were presented. Most interestingly, as shown in Fig. 8, the topographical pattern of alpha

phase synchronization showed large differences between concrete and abstract words already in a very early time window of 100–200 ms. In this early time window (that coincides with the appearance of the P1 component), only for concrete but not abstract words a distinct pattern of stable phase relations was found primarily between leading parieto-temporal and trailing anterior sites, indicating a direction of activation from posterior to anterior brain regions. For abstract words, the number of significant phase relationships dropped considerably (cf. Fig. 8B). Because at this time an acoustically presented word can hardly be identified (mean duration for pronunciation was 760 ms), differences in alpha phase synchronization between word categories most likely reflect differences in global categorization processes between abstract and concrete words. Interestingly, the speed of traveling alpha waves was faster for abstract than concrete words. Because abstract words are less numerous than concrete words, this may indicate that the search area for abstract words can be narrowed down faster for abstract than concrete words.

Taken together, these findings suggest that event-related alpha coherence emerges at the time window of the P1 and reflects the timing of co-activation between brain sites during



**Fig. 8** – Topographic pattern of stable phase relationships in an early time window of encoding acoustically presented nouns (reprinted from Schack et al., 2003, with permission from Wiley). (A) Whereas immediately after the onset of acoustic word presentation (0–100 ms) the network of phase coherence is similar for concrete and abstract nouns, (B) large differences can be observed during a time window of 100–200 ms that coincides with the appearance of the P1 component. Thus, global categorization processes occur very early and precede the identification of a specific word (the average time needed to pronounce a word was 760 ms).

interactive top-down and bottom-up processing. The direction of activation (as measured, e.g., by the direction of phase lag) depends very much on the type of task. If performance of a task relies on general processing characteristics (as, e.g., is the case in the task used by [Schack et al., 2003](#)), the direction is from posterior to anterior sites. If, however, subjects are instructed to perform specific operations from trial to trial (as, e.g., is the case in the manipulation task used by [Sauseng et al., 2005b](#)) traveling direction is from anterior to posterior regions.

Does this mean that alpha may also reflect bottom-up processes? The crucial point here is the definition of what should be understood by 'bottom-up'. We propose to use this term only for early sensory processes that are not yet affected by top-down influences. ERP research suggests that the P1 component (at about 100 ms) represents the earliest time window in which top-down influences can take place. Processes occurring after the time window of the P1 may, thus, already operate under top-down influence, even though the direction of communication between areas may be from 'lower' to 'higher' brain regions.

#### 4. The physiological basis of alpha oscillations

Since several decades, it was suggested that the thalamus plays a key role in the generation of cortical oscillations and sleep spindles in particular ([Andersen and Andersson, 1968](#)). Thus, it was tempting to assume that alpha, as the dominant oscillation in the human scalp EEG, also is generated by thalamic nuclei. This view has led to the idea that the cortex might be passively driven by a 'thalamic pacemaker' (cf. [Basar et al., 1997](#), for a review). The seminal work by [Lopes da Silva et al. \(1973; 1980a,b\)](#), however, has clearly demonstrated that this is not the case (at least in a strict sense) because different alpha oscillations with slightly different frequencies can be recorded from certain cortical areas. Nonetheless, it was demonstrated that certain thalamic nuclei have a strong influence in determining the alpha activity of the cortex. This early work has led to three basic assumptions about alpha that are still valid today: (i) alpha is not generated by a thalamic pacemaker. (ii) Cortical alpha is modulated by a thalamo-cortico-thalamic reentrant network. (iii) Alpha is not a unitary phenomenon, it comprises different oscillations with different frequencies in a broad range. Besides these rather basic aspects, however, almost nothing is known about the physiology of alpha.

Considering the potential importance of the thalamus for the generation of EEG oscillations and the fact that the thalamus and cerebral cortex are closely related, it is obvious that understanding their reciprocal connections might be of crucial importance for a better understanding of alpha. It is a well-established finding that the reticular (RE) nucleus of the thalamus plays a key role in the control of rhythmic EEG activity in the mammalian brain, particularly during sleep ([Lopes da Silva, 1991; Steriade et al., 1990a,b, 1993](#)). The neural network consists of four elements (two inhibitory and two excitatory pyramidal neurons) which form a thalamocortical feedback loop. The neurons of this circuit are GABAergic neurons of the RE nucleus, inhibitory local circuit neurons, thalamocortical (Th-ctx) relay and corticothalamic (Ctx-th)

cells. There is a large and impressive body of animal research focusing on intrinsic membrane properties which can be best studied in vitro (for a review cf. [Steriade, 2001](#)). This line of research has provided detailed insight into the intrinsic neuronal and network properties of spindle oscillations (7–14 Hz), which are generated in the thalamus. Sleep spindles are associated with inhibitory processes in the thalamus and can be regarded as 'gating mechanism' that blocks processing of information from the outside world. But sleep spindles and alpha oscillations are strikingly different phenomena for a variety of reasons.

More recent research, however, starts to shed light on the differences between spindles and alpha. The crucial point here is that thalamic relay cells (i.e., Th-ctx cells) exhibit two distinct response modes which are termed 'tonic' and 'burst mode'. Until recently, it was believed that the burst mode (characterized by synchronized bursts of action potentials) that comprises sleep spindles as well as low-frequency oscillations occurs solely during sleep and the tonic mode (characterized by single spike, tonic, firing) only during alert wakefulness. Recent work, however, has challenged this view and shown that bursts can also be observed in awake animals (e.g., [Sherman and Guillery, 1996](#); for reviews cf. [Sherman, 2001a,b; Nicolelis and Fanselow, 2002](#)). This is a highly important finding because alpha may be related to a burst mode of firing during wakefulness.

The physiology of burst mode firing is well understood. Bursts in Th-ctx cells are triggered when the cell is hyperpolarized and low threshold spikes (LTS) appear which then are followed by bursts of regular (Na) action potentials. Thus, a cell is 'switched' in the burst mode only if a pronounced hyperpolarization develops. It is well documented that in this case sleep spindles can usually be observed (for an extensive review see, e.g., [Steriade, 1999](#)). Because in this case a cell cannot relay (e.g., sensory) information into the cortex, the traditional interpretation is that the 'thalamic gate' is completely closed during the burst mode. Indeed, it is a well-established fact that sleep spindles are a reliable indicator for a person leaving the hypnagogic state (which is the transition period from waking to sleeping) and loosing conscious awareness. However, if one assumes that alpha activity also is generated (or controlled) by bursting Th-ctx cells, the question is whether periods of alpha activity also reflect a state in which no information can be transmitted from the thalamus to the cortex (and connected cortical areas).

[Sherman \(2001a\)](#) argues that both modes, the tonic and the arrhythmic burst mode efficiently relay information in the cortex but have different consequences for information processing. Whereas the tonic mode allows for a more 'linear' and 'faithful' encoding, the burst mode – due to its large signal to noise ratio – is well suited to detect subtle changes in the environment. Impressive empirical evidence for this interpretation comes from studies in which a visual stimulus (a sinusoidal grating that drifts through the receptive field) was presented when geniculate Th-ctx cells were either in the relay or burst mode. The results indicate that during both modes information is relayed to the cortex, but the cortical response is quite different. Surprisingly, during the burst mode cortical cells responded with a much larger EPSP than during the tonic mode ([Swadlow and Gusev, 2001](#)). Thus, the



burst mode may serve as ‘wake up call’ from the thalamus (Sherman, 2001b), reflecting an attentional mechanism, in which certain aspects of stimulus information are relayed. This interpretation is similar to Crick’s ‘searchlight hypothesis’ (Crick, 1984).

The findings described by Sherman (2001a,b), Sherman and Guillery (1996) and Swadlow and Gusev (2001) are based on arrhythmically occurring bursts that cannot be related to alpha activity. Nicolelis and Fanselow (2002), however, reported findings where rhythmical bursting was observed during a state of alert wakefulness that may behaviorally be described as a specific state of attention that may be termed ‘expectant attention’.

#### 4.1. A possible physiological model for alpha?

Nicolelis and Fanselow (2002) have related different types of tactile stimulus processing in the rat thalamus (VPM nucleus) and sensory cortex (SI) to different behavioral states. Because rats use their whiskers to encode tactile information, the observation of whisker movements is important for the classification of different behavioral states. Three types of behaviors were distinguished. A quiet state without whisker movements in which rats are standing or sitting still, a whisker ‘twitching’ state, and a ‘whisking’ state during active exploration of the environment. Whisker twitching is characterized by very rhythmic small-amplitude whisker movements. During whisking, rats move their whiskers back and forth to explore objects and whisker movement is characterized by slow, large-amplitude sweeps with a frequency of about 4–6 Hz. Most interestingly, only during whisker twitching (occurring spontaneously and lasting from several seconds to more than a minute) Th-ctx cells in the VPM are in a rhythmic burst mode and fire bursts of low threshold calcium spikes. In contrast to the quiet and whisking state, large-scale coherent, oscillatory neural activity (between 7 and 12 Hz) can be observed between cells during the twitching state. This synchronous oscillatory activity appears first in the cortex (SI) and later in the thalamus (VPM). Then, after the onset of this oscillation in the thalamocortical loop, the whiskers start to move rhythmically forward and backward with the same frequency as the neural oscillation. This peripheral oscillation is completely coherent with the neural oscillation but is characterized by a consistent phase difference in a way that the forward movement of the whisker precedes the occurrence of a burst by about 30–40 ms. A stimulus presented during this time window has the highest probability (compared to all other behavioral states) to elicit a neural response in the VPM thalamus. Due to intrinsic properties of Th-ctx cells in the VPM, a stimulus presented in a time window (with a width of about 50 ms) preceding this hypersensitive period would have only a small effect because the low threshold calcium channels of Th-ctx cells are inactivated.

According to the suggested inhibition–timing hypothesis our interpretation of the findings reported by Nicolelis and Fanselow (2002) and Fanselow and Nicolelis (1999) is that during whisker twitching a rat is in a state of expectant attention in which a change in the environment (e.g., an approaching animal) is expected. In this state the cortex is not involved in the (bottom-up) processing of information

(as e.g., during whisking) but initiates a top-down process to enhance the encoding of a stimulus when it occurs. This interpretation is supported by several facts. Most importantly, the alpha-like oscillation – most likely the mu rhythm – appears first in the cortex and (via thalamocortical circuits) induces oscillatory whisker movements that serve to sample tactile information. Furthermore, it should be emphasized that hyperpolarization (of Th-ctx cells) for a period of at least 50–100 ms is a necessary requirement that the tonic mode switches to the burst mode. Thus, the initiation and maintenance of the alpha-like oscillation is associated with a period of pronounced thalamic inhibition that plays the crucial role for the timing of the hypersensitive period during which a stimulus has the highest detection probability. This is completely in line with the idea that alpha plays an important role for the timing of neural processes and is consistent with the reported findings about alpha phase-dependent changes in the processing of visual stimuli. Finally, the top-down activation pattern of this alpha-like oscillation is in sharp contrast to sleep spindles which can also be observed when the cortex is removed.

Further evidence for the idea that alpha plays an important role for the timing of neural processes comes from research by Ahissar and colleagues. Ahissar and Kleinfeld (2003) have emphasized that information processing in sensory-motor networks does not obey feedforward computation schemes but depends on large-scale feedback loops. As an example, inconsistent with a feedforward scheme, the phase of thalamic oscillatory activity lags the phase of cortical activity (Nicolelis et al., 1995). Ahissar and Kleinfeld (2003) have shown that this finding is consistent with a closed loop computation scheme consisting of many parallel thalamocortical loops that function as phase-locked loops (PLLs). A PLL is an algorithm used by electrical engineers that is considered an optimal temporal decoder. Ahissar and Arieli (2001) have demonstrated that thalamocortical loops (described as PLLs) are capable of decoding temporal information provided by the rhythmic movement of vibrissae. The accuracy of this movement (Berg and Kleinfeld, 2003) already suggests that phase plays an important role for the encoding of vibrissae position (Kleinfeld et al., 1999). Although part of a closed loop, the cortex and thalamus may serve different functions. Ahissar and Kleinfeld (2003) suggest that cortical oscillatory activity is not driven by sensory events but is generated independently to decode or ‘measure’ the input periodicity, whereas thalamic relay neurons are thought to function as phase detectors.

Although the reported findings appear as ideal model for alpha, as suggested by the inhibition–timing hypothesis, several other findings may question its general validity. As an example the rat VPM lacks local circuit cells. Thus, other thalamic nuclei may show a different type of oscillatory behavior. Another finding potentially not in line with our hypothesis is the detection of gap junctions between a certain type of excitatory thalamic cells that are capable of rhythmic firing in the alpha frequency range (e.g., Hughes and Crunelli, 2005). Most interestingly, these excitatory cells exhibit a very selective connectivity and are activated by excitatory cortical input. Their functional meaning remains an open question and has to be determined in future research.

It should be noted that alpha-like responses were also found in subcortical areas, such as the reticular formation (RF) and the hippocampus (Basar, 1999). Basar et al. (1997) emphasized that the RF exhibits a delayed alpha response (that probably is associated with induced alpha activity). In general, these observations were interpreted in terms of distributed alpha systems in the brain (Basar et al., 1997), but their functional meaning is still an open question. Jones et al. (2000) emphasize that alpha may be generated by local cortical circuits in layer V and that they synchronize as long as there is no delayed external input to these local networks.

Finally, we should also emphasize that one of the most straight forward tests of our hypothesis apparently leads to inconsistent results. The application of benzodiazepines (a GABA agonist) does not lead to increased alpha activity as one would expect if alpha is related to inhibitory activity but instead to a decrease in alpha (Berchou et al., 1986; Fingelkurts et al., 2004; Link et al., 1991; Schreckenberger et al., 2004). On the behavioral level, however, these findings are in line with our hypothesis. The assumption is that the initiation of a top-down process is an active process. Benzodiazepines are well known to make humans drowsy and inattentive. By means of this influence, they may be responsive for the suppression of cortical alpha. In other words, brain processes that initiate or induce a top-down process may be excitatory. Consequently, the inhibition of this excitatory process may be a crucial factor for the benzodiazepine-related suppression of alpha.

## 5. Elaboration of the alpha inhibition-timing (AIT) hypothesis and critical questions

We have focused on two basic aspects, one referring to the state, the other to the timing of information processing. With respect to the first aspect, experimental evidence shows consistently that ERD reaches a maximum during a time window in which (conscious) task-related processes take place, whereas ERS can be observed when certain aspects of task performance are under top-down control. Although both cases reflect states of information processing, their functional difference can be best described in terms of processing selectivity. During ERS selectivity is high, during ERD low. Here, we refer to the general idea that oscillations operate as inhibitory filter to achieve a high signal to noise ratio by allowing only (a comparatively) small number of cells to process information selectively and silencing the majority of other cells. As an example, if a top-down process is initiated to control the execution of a task, large alpha amplitudes will be observed. The duration of ERS may be quite short and transient as, e.g., in the case of evoked alpha during early event-related processing. If, however, a top-down process is initiated to block the execution of a task for some time, ERS will be expected during that time period in which the execution of a task is withheld. Thus, prolonged ERS in tasks requiring not to give a response (e.g., not to give a motor response in the task used by Hummel et al. (2002) or not to retrieve items during a retention period as, e.g., in the task used by Klimesch et al. (1999) may not reflect ‘unspecific’ inhibition but instead a highly specific top-down process that is maintained over a longer period of time. We will term this

‘process-specific’ inhibition and will contrast it from ‘unspecific’ inhibition which may be observed, e.g., during relaxed inactivity or drowsiness. The idea here is that a slight increase in oscillatory activity might silence virtually all cells in the process-relevant assembly and, thus, block selective processing completely. The interesting point here is that both types of inhibitory processes will be reflected by large alpha amplitudes and that the increase of inhibition from a specific to an unspecific state may be quite small and difficult to detect by the scalp EEG. This may explain the paradoxical fact that large alpha can be observed during active cognitive processes and mental inactivity.

The assumption that alpha serves an important function for the timing of cortical processes simply is an extension of our ideas underlying the functional meaning of alpha amplitude for the state of information processing. Oscillations are not only characterized by frequency and amplitude but also by phase and the important fact here is that any oscillation – by necessity – consists of maximal and minimal excitatory (or maximal inhibitory) phases related to the peaks and troughs of the oscillation. Interpretation of the polarity of the peaks and troughs depends on a variety of different factors (such as where the source is and whether inhibitory or excitatory neurons are involved) and cannot be identified unambiguously. Nonetheless, we try the following speculative prediction which is based on the following two facts. First, it is generally assumed that the EEG stems from postsynaptic potentials that are generated in the apical dendritic layer (i.e., cortical layer I, which is closest to the scalp electrode in relation to deeper cortical layers). Second, when considering in addition that excitatory cells are much more abundant in the cortex, a negative potential in the scalp EEG reflects primarily excitatory processes (i.e., increased EPSP activity in layer I) whereas a positive potential reflects a lack of excitatory processes (i.e., decreased EPSP activity in layer I, probably associated with GABAergic input). The few studies on the behavioral effects of alpha phase are consistent with this conclusion (e.g., Dustman and Beck, 1965; cf. Section 4.1). They indicate that if early cortical processing (around 50 ms poststimulus) coincides with the surface negative peak of alpha (reflecting excitatory processes) sensory processing is enhanced.

We have assumed that the P1 is (at least in part) a manifestation of a phase-locked alpha activity caused by phase reset. The function of this phase-locked alpha activity is explained in the sense of process-specific inhibition during the earliest time window in which top-down processes can influence/shape bottom-up processes. Following the P1, excitatory processes within the N1 window probably reflecting early semantic identification are assumed. During this time period of about 100–250 ms an increase in alpha coherence and/or phase synchronization can be observed at process-relevant sites. The direction of activation (as assessed by the direction of alpha phase lag) is from ‘higher’ to ‘lower’ areas if expectancy is helpful, and in the opposite direction if expectancies are lacking. Thus, in both cases alpha will be important for the control of timing and the direction of the spread of cortical processes.

All of the described functions of alpha are based on cases where alpha exhibits large amplitudes and, thus, is not in a

‘desynchronized’ state. Typically, alpha will desynchronize after evoked alpha disappears which is the case after about 200 or 300 ms poststimulus. In other words, in sharp contrast to the traditional belief, active processes that are assumed to be related to alpha occur during the synchronized and not the desynchronized state. This is an interesting conclusion because alpha can thus be considered an oscillation that is physiologically very similar to other well investigated oscillations that typically exhibit large amplitudes during a time they are executing those functions they are supposed to do. Thus, ERD developing beyond about 200 or 300 ms is a sign that the influence of alpha on cortical activation is vanishing and other task-relevant processes (most likely those related to episodic encoding and/or semantic integration and evaluation) take place.

### 5.1. Is ERD really the typical response of alpha?

Because we assume that alpha is an oscillation completely comparable in its behavior to other well described oscillations, the question arises why the typical alpha response is ERD and not ERS (as for delta, theta, frontal midline theta and gamma). The reason may have to do with the fact that alpha is the ‘dominant’ oscillation in the human EEG, exhibiting the largest power usually during a reference or resting period. We have assumed that periods of pronounced alpha reflect either unspecific inhibition or active top-down processes. If these processes are interrupted or terminated, alpha will desynchronize. Thus, the relationship between reference power and the direction and extent of an event-related power change will depend at least in part on two factors, on interindividual differences in cognitive processing strategies but also on task type.

We have found clear evidence that in contrast to the traditional belief, the event-related response of alpha in a picture memory task can either be ERD or ERS depending on interindividual differences in the reference power level. Typically, more subjects have large reference power and, thus – over a sample of subjects – the typical response is ERD although a considerable number of subjects actually exhibit ERS (cf. Klimesch et al., 2004). We have further shown that these differences are related to cognitive performance in a predictable way (e.g., Klimesch et al., 2003).

We already have emphasized in previous sections that differences in reference power may reflect differences in top-down control. Large reference alpha power may reflect unspecific inhibition and will keep the mind from being active. This will be helpful for a typical memory task in which a subject cannot expect whether an old or new item will be presented in the next trial. Thus, preventing active processes may be helpful to prevent interferences and to improve memory performance (Klimesch, 1999). In contrast, if a certain stimulus, e.g., a light flash presented near detection threshold (Ergenoglu et al., 2004) or the letters p or q exposed very briefly and followed by a mask (Hanslmayr et al., 2005a) are to be detected, performance will improve if the cortex already is activated (or preactivated) in the reference period. Consequently, small reference alpha power will be related to good perceptual performance (cf. Fig. 7E).

### 5.2. Alpha and the interplay between other frequencies

We have found evidence that alpha plays an important role in short-term memory tasks (cf. Section 3.2.1) but have at the same time assumed that upper alpha oscillations may be considered a functional correlate of a LTM system. If short-term storage would be a process completely different from LTM storage, our findings would indeed represent conflicting evidence. If, however, upper alpha oscillations – in combination with theta (an oscillation well known to be related to WM demands; cf. Klimesch, 1999) – reflect short-term storage in the sense that they allow controlled access to LTM codes, there is no contradiction with earlier findings. Analyzing upper alpha and theta phase in a memory scanning task (Schack et al., 2005) revealed that already during retention a significant increase in alpha:theta phase coupling could be observed (between posterior alpha and frontal theta) that exhibited a further increase during the first 300 ms after the presentation of a probe. We have interpreted this finding to exhibit an interplay between WM and LTM in a sense that alpha controls access to LTM traces that are used (‘reactivated’) for short-term storage (cf. Ruchkin et al., 2003). The findings reported by Sauseng et al. (2002) provide further evidence for this view (cf. Section 3.5 and Fig. 5).

Because gamma generally is associated with perceptual processes, we would expect that phase coupling between alpha and gamma reflects the early top-down influence of alpha on perceptual processes. To our knowledge, there are no studies yet on this specific issue, although the findings by Klopp et al. (2000) and Von Stein et al. (2000) are quite suggestive. Nonetheless, it has been demonstrated that gamma also exhibits evoked activity in a very early time window that overlaps with evoked alpha (Herrmann et al., 2004c). Our hypotheses about the functional role of alpha are well in line with the memory match and utilization model for gamma, proposed by Herrmann et al. (2004b). They explain the early (evoked) gamma band response (around 80–100 ms) in terms of a match between bottom-up and top-down processes. The interesting point here is that also according to their findings the time window for the interaction between bottom-up and top-down processing is around 100 ms. With respect to the functional role of alpha and gamma, it appears likely that specific types of sensory information (such as the existence of continuous contour lines in pictures as compared to scrambled pictures) allows for early classification processes (reflected by gamma oscillations) that interact with more global semantic categorization processes (reflected by alpha).

### 5.3. Alpha activity: an epiphenomenon?

The inhibition-timing hypothesis implies an active and causal role of alpha for information processing. Findings about driven alpha activity and SSVEPs (cf. Section 3.6.1), however, could be interpreted as evidence that alpha is a passive resonance phenomenon. As an example, it is well known that the driven response (regardless of being elicited by an unstructured or structured stimulus) shows the largest amplitude at a frequency of alpha at about 10 Hz (e.g., Mast and Victor, 1993; Kawaguchi et al., 1993; Sakamoto et al., 1993;



Shils et al., 1996; Lakie and Combes, 1999; Lazarev et al., 2001; Herrmann, 2001). Furthermore, the amplitude of the driven response depends on IAF. As an example, Gebber et al. (1999) have reported that for a subject with IAF=10.8 Hz and a stimulus frequency of 4.9 Hz, the response at the first harmonic (9.8 Hz) shows the largest amplitude, the response at the fundamental (4.9 Hz) the second largest amplitude, whereas the amplitude of spontaneous alpha exhibits the smallest amplitude.

If alpha is nothing but a passive resonance phenomenon of our brain, any changes in alpha (transiently induced by external events, such as flicker or other methods) should have no effects on cortical or cognitive processes. It is very important to emphasize that this question has not been addressed within the SSVEP approach, because the influence of flicker frequency on cognitive performance was never investigated. The relationship with cognitive processes was assessed only indirectly by studying cognition-related changes in steady-state evoked potentials in selected frequency domains.

The crucial question, thus, is whether an externally induced change of alpha activity also leads to changes in cognitive processes. We have tested this question by using rTMS at IAF to improve memory performance (Klimesch et al., 2003). In a series of studies, we have shown (for a review, see Klimesch, 1999) that good memory performance is related to large alpha reference power (i.e., large power preceding task performance), decreased test power (i.e., small power during task performance) and consequently to a large ERD. The hypothesis was that inducing rhythmic activity into the cortex by a brief series of TMS pulses with a frequency at individually adjusted upper alpha (IAF+1) will increase cognitive performance and change alpha activity in a way, we know is typical for good performance. Because good performance is related to large reference alpha activity, we applied rTMS at IAF during a reference interval preceding task performance. We used a mental rotation task and applied rTMS at IAF+1 Hz over a frontal (Fz) and a right parietal site (P6). Control conditions were rTMS at IAF – 3 Hz (lower alpha, individually adjusted) and at 20 Hz (beta frequency, not adjusted individually).

The findings indicate that only rTMS delivered at IAF+1 leads to a significant improvement in performance (with respect to accuracy but not speed of mental rotation) when compared with sham. Furthermore, the influence of rTMS at IAF+1 on alpha activity mimicked exactly that situation which we know is typical for good performance: increased reference power, decreased test power and, consequently, a large ERD. Similar findings were obtained when using neurofeedback training instead of rTMS (Hanslmayr et al., 2005b).

The conclusion is that inducing a transient change in alpha activity (by means of external stimulation or neurofeedback) inevitably leads to a change in cognitive performance in a predictable way. Thus, these findings suggest that the relationship between alpha and cognitive performance is not correlative but causal in nature. Consequently, we have to assume that the use of a flicker also will have an impact on cognitive processes. There is supportive evidence, as the findings from Williams (2001) indicate. He observed that words presented with a flicker at 10 Hz were better remem-

bered in a later performed recognition task than words presented at lower or faster frequencies. Findings about flicker in the gamma frequency range also suggest that flickering stimuli with a certain frequency influence perceptual performance (Elliott and Müller, 1998, 2000; Elliott et al., 2000).

## 6. Conclusions

The general line of our argumentation is that alpha – like other oscillations – is an active phenomenon but reflects – in contrast to other oscillations, a certain type of top-down process. The active role of alpha is seen in a mechanism that also may underlie the functional role of other oscillations: Synchronization in the alpha frequency range helps neurons in distributed networks to effectively activate common target cells. We think that this timing mechanism plays an important role in the top-down control of cortical activation. Traveling alpha waves, cyclic changes in cortical excitability in the alpha frequency range, alpha coherence, phase synchronization and phase locking are considered manifestations of this timing mechanism.

The assumption that alpha reflects inhibition may – at the first glance – appear contradictory to the view that alpha plays an active role in information processing. But the idea is that inhibition is an important factor that controls the exact timing of an oscillation. Thus, inhibition helps to establish a highly selective activation pattern.

Top-down control probably is not a unitary phenomenon. Different types of processing systems, such as WM and (sensory-semantic) LTM may have their own types of top-down processes. We assume that upper alpha oscillations are related to top-down processes in a complex sensory-semantic LTM system that controls the access to and manipulation with stored information. As an example, when a task requires that certain types of processes must be performed with stored information (e.g., stored information must be kept in mind, must not be retrieved or must be manipulated by performing some transformation) alpha synchronizes over respective brain areas. However, as soon as the memory trace actually is retrieved (or a perceived stimulus is semantically categorized) which is a process requiring a few 100 ms (depending on task difficulty and other factors) alpha starts to desynchronize. We assume that during this early period of stimulus encoding, phase-locked alpha reflects the top-down influence of semantic categorization processes.

Several factors may be similar for the generation of different types of oscillations. Inhibition and intrinsic time constants are well-known examples. Nonetheless, the exact mechanisms for generating an oscillation may differ widely between different types of oscillations such as theta, alpha or gamma, depending on network properties, cell types, cell physiology and other factors. Thus, for a better understanding of the functional role of oscillations the investigation of their functional interplay may be of crucial importance. This view has been emphasized by several investigators (Basar et al., 2004) and first results appear promising (e.g., Palva et al., 2005; Schack et al., 2005).

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