# Event-related alpha and theta responses in a visuo-spatial working memory task

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## Abstract

**Objective**: To explore the reactivity of the theta and alpha rhythms during visuo-spatial working memory.

**Methods**: One hundred and seventy-four subjects performed a delayed response task. They had to remember the spatial location of a target stimulus on a computer screen for a 1 or a 4 s retention interval. The target either remained visible throughout the entire interval (sensory trials) or disappeared after 150 ms (memory trials). Changes in induced band power (IBP) in the electroencephalogram (EEG) were analyzed in 4 narrow, individually adjusted frequency bands between 4 and 12 Hz.

**Results**: After presentation of the target stimulus, a phasic power increase was found, irrespective of condition and delay interval, in the lower (roughly, 4–8 Hz) frequency bands, with a posterior maximum. During the retention interval, sustained occipital–parietal alpha power increase and frontal theta power decrease were found. Most importantly, the memory trials showed larger IBP decreases in the theta band over frontal electrodes than the sensory trials.

**Conclusions**: The phasic power increase following target onset is interpreted to reflect encoding of the target location. The sustained theta decrease, which is larger for memory trials, is tentatively interpreted to reflect visuo-spatial working memory processes. © 2002 Elsevier Science Ireland Ltd. All rights reserved.

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## 1. Introduction

Recently there has been a growing interest in the relationship between memory processes and event-related changes in theta power in the human, scalp-recorded electroencephalogram (EEG). In a number of experiments, Klimesch and coworkers studied changes in EEG theta power during the performance of episodic and semantic memory tasks (cf. Klimesch, 1996, 1999 for reviews) with a variant of a method known as event-related desynchronization (ERD; Pfurtscheller and Aranibar, 1977). This analysis method, the so-called induced band power (IBP; Klimesch et al., 1998) method, quantifies the event-related changes in amplitude of frequency-specific EEG rhythms, such as theta, alpha or beta/gamma rhythms.

Typically, in the studies by Klimesch and coworkers (see Klimesch, 1996, 1999 for reviews), subjects read a word list, or had to perform a semantic judgment task. Subsequently they were asked to perform either a free or a cued recall task. These experiments convincingly demonstrate that both the encoding and the retrieval of episodic information are accompanied by an event-related increase in theta power, which is larger for good than for poor memory performers (e.g. Klimesch et al., 1990, 1996, 1997a). For example, Klimesch et al. (1997b) asked subjects to judge the semantic congruency of feature–concept pairs (such as claws–eagle). After that, an episodic memory task was performed, in which subjects had to recall the concept word that was actually paired with a feature word in the initial list. The authors found that only recalled words were associated with a significant theta power increase. Moreover, this effect was only present for the high memory performers.

In additional studies, it was shown that event-related increases in theta power are generally larger during retrieval than during encoding (e.g. Klimesch et al., 1994, 1997c). For example, in a recent study (Klimesch et al., 2001), subjects viewed 70 pictures in the study phase of the experiment. After about 6 min, subjects were asked to make a recognition judgment for 60 previously seen pictures (targets) and 120 distracters. Whereas baseline (i.e. pre-

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stimulus) levels of theta power were similar during the study phase and the test phase prior to the presentation of both targets and distracters, post-stimulus theta power increased by approximately 50% (relative to pre-stimulus theta power) during the study phase (encoding) of the experiment. During the test phase (retrieval), theta power increases relative to the pre-stimulus interval were in the range of 100–150% for correctly identified targets and distracters. An increase in theta power during memory retrieval has also been observed by Burgess and Gruzelier (1997, 2000) during the recognition of both words and faces.

These data strongly suggest that phasic theta power increases are related specifically to encoding and retrieval processes, with retrieval generally yielding the largest theta increases. However, as a result of a renewed interest in the relation between theta activity and cognitive processes (e.g. Kahana et al., 2001), other studies have been performed which cast some doubt on this highly specific interpretation of the phasic theta increase identified by Klimesch and co-workers. Krause et al. (2000) asked subjects to perform a typical working memory (WM) task, namely a visual sequential (backward) letter detection task, in which memory load was varied from zero to two items. Although specific effects of WM load were present only in higher (that is, 6–8 and 8–10 Hz) frequency bands, an event-related increase in theta power was present in the interval in which WM processes were active. The latter effect was interpreted by the authors to reflect stimulus identification or WM processes. These results indicate that an increase in theta power is not uniquely related to the *long-term* encoding and/or retrieval of episodic information, but also to WM operations, which at a general level involve *short-term* storage, manipulation, and utilization of mental representations (e.g. Levy and Goldman-Rakic, 2000).

It is, however, overly simplistic to treat WM as a unitary concept. Instead, one has to distinguish between different aspects of WM. First, some authors have suggested a process-specific distinction between maintenance and active manipulation of information in WM, supported by ventral and dorsal prefrontal cortical regions, respectively (Owen et al., 1999). Second, the proposal that different neuroanatomical substrates exist for different domains, such as spatial, verbal and object WM (Goldman-Rakic, 1998) is supported by an increasing body of evidence (see, for example, Carpenter et al., 2000; Postle et al., 2000). In the light of these findings, an interesting question is whether the theta response identified by Krause et al. (2000) is sensitive to different subdomains of WM. In the study by Krause et al. (2000), subjects were engaged in a WM task in which verbal material had to be maintained in WM. In order to have a more complete understanding of the relationship between theta reactivity and WM processes, it would be desirable to identify theta responses to WM processes in other domains as well.

Gevins and co-workers (Gevins et al., 1997; McEvoy et al., 2001) found theta power increases during tasks engaging spatial WM. However, they evaluated *task-related* changes, i.e. contrasting the power in a resting condition with the power in an active condition, a procedure which eliminates any temporal resolution from the analysis. This makes it difficult to specifically attribute the power changes to WM processes.

The present paper aims at identifying *event-related* changes in EEG power in the theta frequency band related to the execution of a visuo-spatial WM task. In addition to the theta band, we also studied the alpha band, for two reasons: first, the results by Krause et al. (2000) suggest that the lower alpha band (roughly, between 6 and 10 Hz) might also show reactivity to WM processes. Second, studying more frequency bands will allow us to assess whether the effects are frequency-specific or a result of broadband power changes.

We used a human adaptation of the classic delayed response task (DRT) often used in animal research. In the classic DRT, the animal is required to remember the location of a reward until a response is permitted (Jacobsen, 1935; Fuster, 1991; see Geffen et al., 1997 for a literature review). In the human version, subjects are required to fixate on a central spot on a touch-sensitive computer monitor. A target, whose location needs to be remembered, is presented in the periphery. After a delay (either 1 or 4 s, in order to manipulate the WM load), the fixation stimulus disappears, and subjects have to respond by touching the screen at the location of the target. 'Sensory' trials, in which the target remains visible on the screen, are randomly intermixed with 'memory' trials, in which the target disappears 150 ms after its appearance. Thus, the sensory trials form a control condition in which task demands are highly similar to those in the memory trials.

The present experiment has been performed as part of a larger research project investigating the role of genetics in adult brain function (cf. Wright et al., 2001; Posthuma et al., 2001a). As genetic studies involve large numbers of genetically related subjects (i.e. about 600 subjects in the above project), a large number of subjects was also available for the present study ($N = 174$ genetically unrelated subjects). Previous studies investigating WM effects using the IBP method have generally not included over 25 subjects. A larger sample size will increase the power of testing for multiple effects as well as the generalizability of the results.

## 2. Methods

### 2.1. Subjects

From the complete pool of 594 familially related subjects that were tested in the larger genetic study, we randomly selected one subject from each family, thus yielding a set of familially unrelated subjects. Of this set, the 174 subjects who had a minimum of 10 correct and artifact-free trials in each condition of the WM task (see below) constituted the

present subject sample. The mean age of this sample was 36.7 (SD 12.89) years. Seventeen subjects were left-handed and 157 were right-handed. Seventy-seven subjects were males and 97 were females.

## 2.2. EEG recordings

The EEG was recorded with 19 Ag/AgCl electrodes mounted in an electrocap. Standard 10-20 positions were F7, F3, Fz, F4, F8, T3, C3, Cz, C4, T4, T5, P3, Pz, P4, T6, O1, and O2. Additionally F1 and F2 were placed halfway between F3 and Fz, and between Fz and F4, respectively. Software-linked earlobes (A1 and A2) served as reference. The vertical electro-oculogram (EOG) was recorded bipolarly between two Ag/AgCl electrodes on the outer right canthus and 1 cm above the eyebrow of the right eye. The horizontal EOG was recorded bipolarly between two Ag/AgCl electrodes affixed 1 cm left from the left eye and 1 cm right from the right eye. An Ag/AgCl electrode placed on the forehead was used as a ground electrode.

Impedances of all EEG electrodes were kept below 3 kΩ, impedances of the EOG electrodes below 10 kΩ. The EEG was amplified (0.05–30 Hz), digitized at 250 Hz and stored for offline processing. The data were later resampled to 256 Hz for practical purposes. Next an automatic artifact detection was performed, discarding trials that deviated more than 75 μV from the 250 ms baseline preceding each trial. For the short delay trials, artifact detection took place in a window of 500 until 1500 ms after trial onset, for the long delay trials in a window of 500 until 4500 ms after trial onset. These time periods correspond to the retention interval, which is the interval starting from target offset (memory conditions only) to the offset of the fixation stimulus, indicating that a response can be made (see below).

## 2.3. Apparatus

During the EEG measurements, the subjects were seated in a comfortable reclining chair in a dimly lit, sound-attenuated electrically shielded room. A touch-sensitive computer screen was placed in front of them. The chair was adjusted such that the center of the screen was at eye-level. Task instruction was given on a written sheet.

For responding, subjects used a rubber tipped pointer (5 mm diameter) to touch the touch-sensitive screen. The pointer was held like a pen, in the preferred hand. Before the trial starts, subjects had to place their hand on a $5 \times 5$ cm$^2$ response pad placed centrally in front of them, 20 cm before the screen. The screen background was dark gray. A black hood with a 205 mm diameter hole in the middle was fastened to the monitor face to ensure that targets at all locations were at an equal distance from the edge of the screen.

## 2.4. Experimental design

In Fig. 1, the time course of an experimental trial is schematically depicted. Each trial started with an auditory Warning Signal (WS, 100 ms, 100 Hz). At WS offset, a black fixation square (diameter = 0.5 cm, visual angle 0.5°) was presented at the center of the screen. At 250 ms after onset of the fixation square, the target, a checkered black circle (diameter = 1.5 cm, visual angle 1.5°) was presented anywhere on an annulus (9.25 cm, 9.25° radius) from the fixation square, except for 4 symmetrical 15° areas around the vertical and horizontal meridians. The target disappeared after 150 ms (memory trials) or remained visible until the end of the trial (sensory trials). In the short delay trials, the fixation square disappeared 1150 ms after target onset, whereas in the long delay trials the fixation square disappeared 4150 ms after target onset. The disappearance
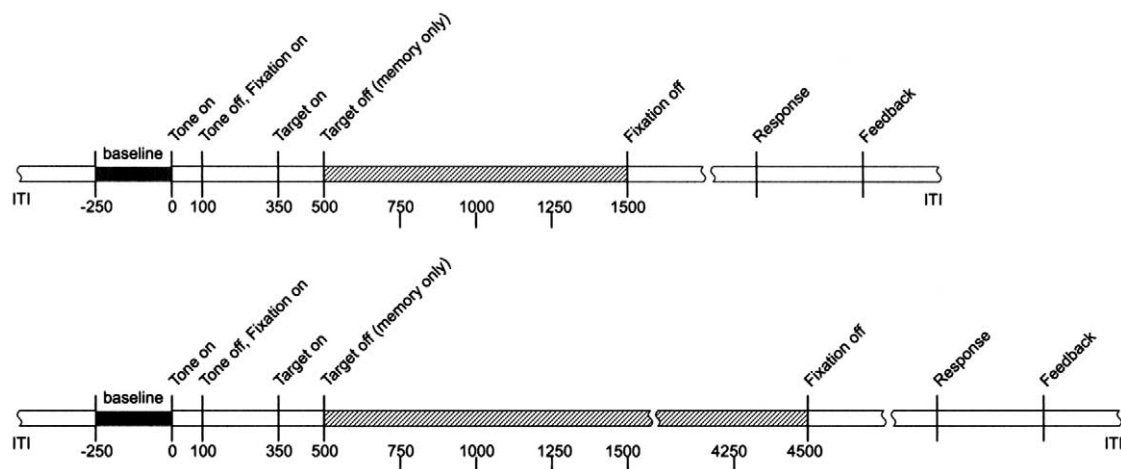


Fig. 1. Schematic representation of the time course of one trial, shown separately for the 1 s (upper row) and the 4 s (lower row) delay interval conditions. The interval marked in dark gray corresponds to the reference interval for the IBP analyses, the interval marked in light gray corresponds to the memory delay interval.

of the fixation square indicated to the subject to lift his hand from the response pad and touch the screen as accurately and as fast as possible. Orthogonal crossing of the memory/sensory and the delay manipulations led to 4 experimental conditions: sensory 1 s delay (S1); sensory 4 s delay (S4); memory 1 s delay (M1), and memory 4 s delay (M4). In addition to the memory/sensory and the short/long delay manipulation, there was a distracter manipulation. A distracter, identical to the target, was presented anywhere in the annulus but not within a 15° radius of the target position. Distracters lasted 150 ms with an onset of 300–700 ms after target onset. In the present paper, only the conditions without distracters are considered.

Before the actual experimental run, there was a 10 min training session. The actual task consisted of two 120-trial blocks, lasting about 14 min each. Within each block, there were 48 sensory trials and 64 memory trials. Half of the memory trials and half of the sensory trials had a short delay (1 s), while the others a long delay (4 s). In 112 trials of each block, targets were presented in either left or right, top and bottom visual fields (i.e. 7.5° off the vertical and horizontal meridians). In each block, there were 8 trials in which the target was presented within the meridian areas. These catch trials were not analyzed. Within each block the order of presentation of the total set of the 120 possible trials was randomized once, and was of the same order for each subject.

For a trial to be correct at the behavioral level, the hand needed to be lifted between 0.1 and 1.5 s after fixation offset, and the screen had to be touched within 1.5 and 3 s after fixation offset within a radius of 2 cm of the target center. Spatial accuracy was monitored by applying the following rules for earning or losing points: Touching within the center target area (0.4 cm) earned 10 points, off target responses earned 8 (0.4–0.8 cm), 6 (0.8–1.2 cm), 4 (1.2–1.6 cm) or 2 (1.6–2 cm) points. Touching outside of the target area lost 5 points and a red error message INCOR-RECT was displayed. Lifting the hand before offset of the fixation spot caused TOO FAST to be displayed. If the maximal response time of 1500 ms expired, TOO SLOW was signaled. All feedback was displayed 25 ms after touching the screen, in the center of the screen, for a period of 1500 ms. This included a running total of the winnings so far, and the amount of points won or lost at the preceding trial. After feedback offset, an intertrial interval of 250–750 ms was followed by onset of the next trial.

### 2.5. IBP computation

For the computation of the IBP changes, we followed the approach outlined by Klimesch (e.g. Klimesch, 1999). In this carefully developed approach, the IBP is computed in individually adjusted narrow frequency bands, based on the individual alpha peak frequency (IAF). The IAF ($M = 9.9$ Hz, SD $= 0.97$) was determined through a spectral analysis on the EEG collected during a 3 min resting period with eyes closed that followed the delayed-recall task (see also Posthuma et al., 2001b). The EEG data were filtered with a fast Fourier transform (FFT) filter in the 4 different frequency bands thus obtained: theta (IAF-6 to IAF-4), lower-1 alpha (IAF-4 to IAF-2), lower-2 alpha (IAF-2 to IAF) and upper alpha (IAF to IAF + 2). Next, for each frequency band the data were averaged, and the resulting (filtered) ERP was subtracted from each single trial in order to avoid a contamination of the IBP measures with the ERPs (see Kalcher and Pfurtscheller, 1995; Klimesch et al., 1998 for a detailed description of this method and its rationale). The single-trial data thus obtained were transformed into power values by squaring the amplitudes, and averaged over time intervals of 250 ms each in order to obtain reliable power estimates. Subsequently the data were averaged over trials, and IBP was computed as the percentage power increase or decrease for a particular time interval in a particular frequency band, relative to a reference interval from 250 to 0 ms preceding trial onset. Finally, the IBP changes were averaged over all subjects for display purposes. In order to avoid confusion, it must be emphasized that a positive IBP percentage indicates a power increase, whereas a negative IBP percentage indicates a power decrease, according to the most recent definition by Pfurtscheller (1999).

### 2.6. Statistical analyses

#### 2.6.1. Behavioral data

Two behavioral measures were analyzed: percent correct responses and spatial accuracy, the latter being quantified as the total amount of points a subject held at the end of the experiment. For both measures, an analysis of variance (ANOVA) for repeated measures was performed with the factors Condition (sensory, memory) and Delay (1 and 4 s).

#### 2.6.2. Physiological data

For the statistical analyses of the IBP changes, the electrodes were grouped into 4 quadrants, each including 3 electrodes: left anterior (LA), including electrodes F7, F3, C3; left posterior (LP), including electrodes T5, P3, O1; right anterior (RA) and right posterior (RP), including the homologous electrodes over the right hemisphere. The rationale for this grouping was that a visual inspection of the data showed that there were only low spatial frequencies (i.e. widespread scalp distributions) in the results. Therefore the grouping of electrodes into quadrants was done, which simplify the analyses. These 4 quadrants were entered into the ANOVAs as two factors, namely Anteriority (anterior, posterior) and Hemisphere (left, right).

The first 1000 ms of each condition were analyzed simultaneously with the following within subjects factors: Delay (1000 or 4000 ms), Condition (sensory, memory), Epoch (4 subsequent epochs of 250 ms each starting at 500 ms from trial onset, which corresponds to the start of the retention interval), Anteriority (Anterior, posterior) and Hemisphere

(Left, Right). The Delay factor served as a control in the analyses of the first 1000 ms. Two between-subjects factors were used: Sex (male, female) and Handedness (right, left).[1] This analysis (termed Analysis I hereafter) was repeated separately for each of the 4 frequency bands considered.

Second, the two long delay conditions (S4 and M4) were compared in a separate analysis in which the entire 4 s delay was analyzed in 1 s periods obtained by averaging IBP values in 4 subsequent 250 ms intervals. Within factors were Condition (sensory, memory), Second (4 subsequent epochs of 1 s each starting at 500 ms from trial onset, which corresponds to the start of the retention interval), Anteriority (Anterior, posterior) and Hemisphere (Left, Right). Between-subjects factors were Sex (male, female) and Handedness (right, left). Again, this analysis (termed Analysis II hereafter) was repeated separately for each of the 4 frequency bands considered.

The rationale for this analysis structure is that Analysis I allows us to study the first 1000 ms with relatively high temporal detail (250 ms epochs) and in a larger number of trials (pooling over the 1 s and the 4 s delay conditions, provided that the factor Delay did not reach significance), and to explicitly compare the S1 with the S4, and the M1 with the M4 conditions. Analysis II, on the 4 s delay conditions only, focuses on the temporal evolution of the effects in the longer retention intervals with larger time steps (1000 ms).

Because of the relatively large number of analyses (4 frequency bands × 2 analysis types), all tests were conducted against an alpha level of 0.01. Where necessary, degrees of freedom (df) were corrected with the Greenhouse–Geisser epsilon, and corrected df and $P$-values are reported. Significant interaction effects were clarified either by post-hoc contrasts, or by breaking them down into simple effects tests, and were tested against Bonferroni corrected alpha levels.

## 3. Results

### 3.1. Behavioral data

In condition S1, the average percentage of correct trials was 95% (SD 9.26), in S4 90% (SD 6.34), whereas in M1 and M4, the percentages were 86.6% (SD 9.40) and 76.8% (SD 11.82), respectively. The analysis on these percentages indicates that regardless of retention interval, subjects performed better on sensory than on memory trials (main effect of Condition: $F_{1,173} = 187.43$, $P < 0.001$). A main effect of Delay ($F_{1,173} = 21.18$, $P < 0.001$ indicated that regardless of Condition, subjects performed better in trials with 1 s delay than on trials with 4 s delay. Finally, an

interaction of Condition with Delay ($F_{1,173} = 188.47$, $P < 0.001$) indicated that the effect of delay was larger in the memory conditions than in the sensory conditions.

Similar results were found with respect to spatial accuracy. The average number of points collected at the end of the experiment was 237.8 points (SD 36.7) for S1, 218.7 points (SD 43.75) for S4, 143.9 points (SD 46.0) for M1, and 101.5 points (SD 53.0) for M4. Again, in the analysis both main effects (Condition: $F_{1,173} = 691.50$, $P < 0.001$; Delay: $F_{1,173} = 28.75$, $P < 0.001$) and the interaction of Condition with Delay ($F_{1,173} = 210.18$, $P < 0.001$) were significant, and their interpretation similar to that of the analysis on percent correct responses.

### 3.2. Physiological data

Figs. 2–5 show the grand average time series of the IBP changes for selected electrodes, as well as topographical representations of the IBP changes at selected time points, for the sensory and memory conditions, separately for each of the 4 frequency bands studied. As expected, analysis I indicated that no statistically significant differences in IBP were present in any of the bands between the first second of the retention intervals of S1 and S4 trials, and M1 and M4 trials (see below). Therefore, only the conditions in which the retention interval was 4 s (that is, S4 and M4) are displayed in the figures. Table 1 lists the significant main and interactions effects, of all within-subjects factors, of the omnibus tests for analyses I and II. Where necessary, $F$ and $P$-values for follow-up tests are given in the text.

#### 3.2.1. Short-lasting IBP changes following target presentation

A visual inspection of Figs. 2–5 suggests that at the beginning of the retention interval, i.e. during (sensory conditions) or immediately after (memory conditions) presentation of the target stimulus, a short-lasting IBP increase can bee seen in the lower frequency bands (theta and lower-1 alpha). This effect is present at posterior electrodes only. Statistically, this effect is expressed in Analysis I, by an interaction between Anteriority and Epoch in these frequency bands, indicating that posterior sites show a larger IBP increase in the first 250 ms after target offset. Although visual inspection of the data, especially the central and parietal channels in Fig. 2, suggests that the phasic IBP increase in the lower frequency bands is larger for sensory than for memory conditions, this is not supported by the statistical analyses. Therefore, the effect can be considered to be task-related (i.e. independent of experimental condition).

In the higher frequency bands, the only significant effects in analysis I involve between-subjects factors, and are therefore not of interest for the present purpose.

#### 3.2.2. Sustained task-related effects

In the theta and lower-1 alpha bands, irrespective of

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[1] Note that the between-subject factors Sex and Handedness were incorporated in the analyses mainly in order to reduce possible error variance due to these factors. The effects involving these factors are not reported, since individual differences are not the main focus of the present paper.
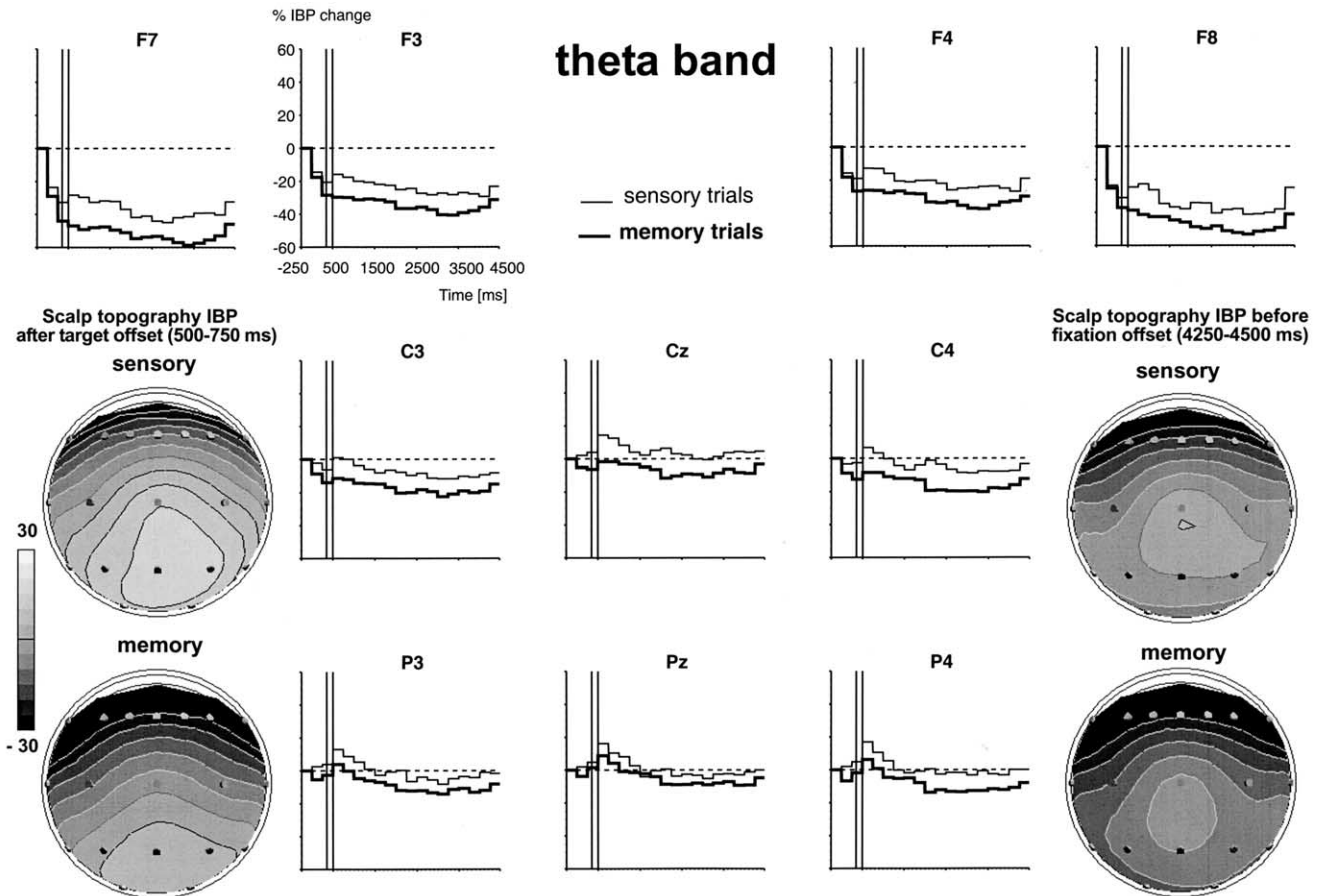
Fig. 2. Time courses at selected electrodes, and topographic maps at selected time points, of the percent induced band power (IBP) changes in the theta frequency band in the S4 and M4 conditions. For the time course plots, vertical lines indicate onset and offset of target stimulus (offset only for memory conditions). IBP changes are shown from 250 ms preceding trial onset to the end of the memory delay interval. For the topographical maps, IBP decrease is represented by dark gray surrounded by white contour lines, IBP increase by light gray surrounded by black contour lines. Gray contour lines correspond to zero power change. Spacing of contour lines is 5% IBP change.

condition, there is a power decrease at anterior electrode positions, which starts at or around target presentation, and which lasts throughout the entire retention interval. Statistically this is expressed in significant main effects of Anteriority both in Analysis I and in Analysis II. Simple effects tests confirm that the power decrease is restricted to anterior sites: in both frequency bands the power decrease differs significantly from 0 at anterior sites, both in Analysis I and in Analysis II (all $P$ values $<0.001$), while at posterior sites, this was not the case (all $P$ values $>0.3$). While the power decrease remains stable throughout the retention interval in the lower-1 alpha band, it gradually increases in magnitude in the theta band, as indicated by a main effect of the factor Second in analysis II of the theta band. Finally, an interaction of Anteriority × Hemisphere in analysis I of the lower-1 alpha band indicates that in this frequency band, the anterior power decrease was larger over the left than over the right hemisphere (15.3 vs. 9.6%, respectively; simple effect of hemisphere at anterior positions: $F_{1,170} = 10.74$, $P = 0.001$).

In the higher frequency bands (lower-2 and upper alpha),

the picture is different. Here a power *increase* can be observed in both frequency bands, which gradually develops from the 1st to the 4th second (respectively, $-8.0$, 2.3, 6.0 and 6.6% power change for the lower-2 alpha band, and $-4.3$, 3.6, 5.2 and 7.2% power change for the upper alpha band). This is expressed in main effects of the factor Second in analysis II of both frequency bands. Finally, an interaction of Second with Anteriority in analysis II of the upper alpha band indicates that the power increase in this band is present only over posterior electrodes (see Fig. 5). Although visual inspection of Fig. 4 suggests that the same is true for the lower-2 alpha band, the absence of an interaction Second × Anteriority in this band indicates that this visual inspection is not supported statistically.

*3.2.3. Differences between sensory and memory conditions*

Most importantly for the present purpose, a visual inspection of Figs. 2 and 3 suggests that in the theta and lower-1 alpha bands, there is a clear IBP decrease in the memory conditions relative to the sensory conditions, which is absent in the higher frequency bands (Figs. 4 and 5). This
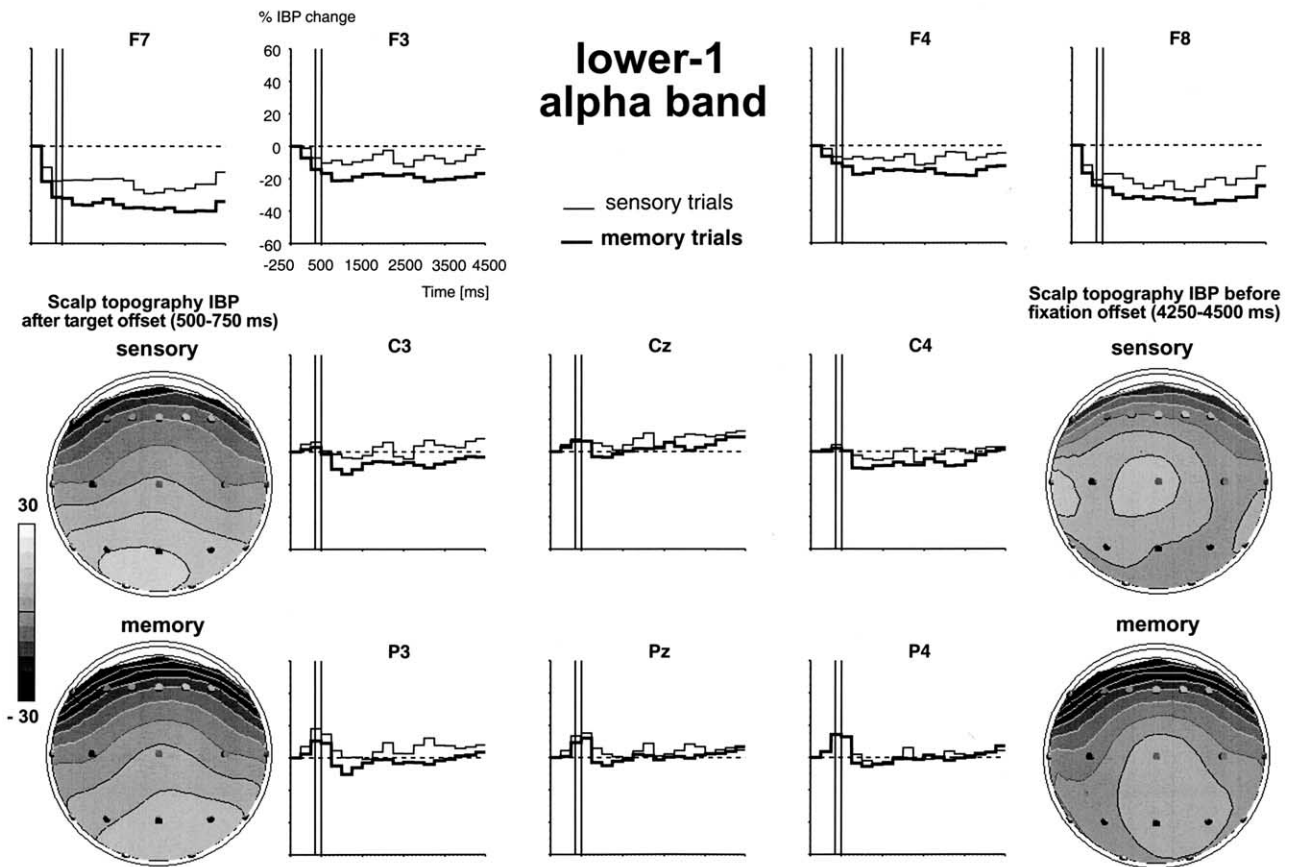
Fig. 3. Time courses at selected electrodes, and topographic maps at selected time points, of the percent induced band power (IBP) changes in the lower-1 alpha frequency band in the S4 and M4 conditions. See Fig. 2 for further details.

effect is supported by the statistical analyses by the main effects of Condition in the lower frequency bands, both in analysis I and in analysis II. The percentages power change for the theta and lower-1 alpha bands are given in Table 2.

## 4. Discussion

In order to explore the possibility of a functional role for the theta and alpha rhythms in visuo-spatial WM, we investigated the IBP changes in the theta and alpha frequency ranges of the EEG during the performance of a delayed response task, for a large number of subjects ($N = 174$). Statistical analyses on the IBP changes demonstrated the presence of 3 effects. First, after the presentation of the target stimulus, a phasic IBP increase is present in the theta and lower-1 alpha bands, over posterior areas, both in memory and in sensory conditions. Second, in both memory and sensory conditions, a sustained *decrease* in IBP is present at anterior electrodes for the theta and lower-1 alpha bands throughout the retention interval, which becomes stronger towards the end of the retention interval in the 4 s delay conditions. At the same time, in the lower-2 and upper alpha bands an IBP *increase* is present over central and posterior sites, which gets stronger

towards the end of the 4 s retention interval. Third, and most importantly, an enhanced IBP decrease is present in the memory trials compared to the sensory trials, at frontal electrodes, in the theta and lower-1 alpha bands only. In the following, we will consider possible interpretations of these effects in some detail, starting with the task-related effects and ending with the WM-related effects, which are the main focus of the paper.

However, before turning to possible interpretations, it should be noted that the present data are not in agreement with the functional distinction between the 4 narrow frequency bands that has been suggested (and repeatedly demonstrated) by Klimesch (1999). Rather, highly similar effects were found in the theta and lower-1 alpha bands on the one hand, and in the lower-2 and upper alpha bands on the other hand. Possibly this could be due to differences in frequency sensitivity between episodic memory processes and (visuo-spatial) WM processes. Given that the average IAF in the present study was 9.9 Hz, the theta and lower-1 alpha bands together correspond on the average to a frequency band of 3.9–7.9 Hz, while the lower-2 and upper alpha band together correspond on the average to a frequency band of 7.9–11.9 Hz. These frequency ranges are fairly in line with the classical definition of the theta and alpha frequency ranges (e.g. Noachtar et al., 1999). There-
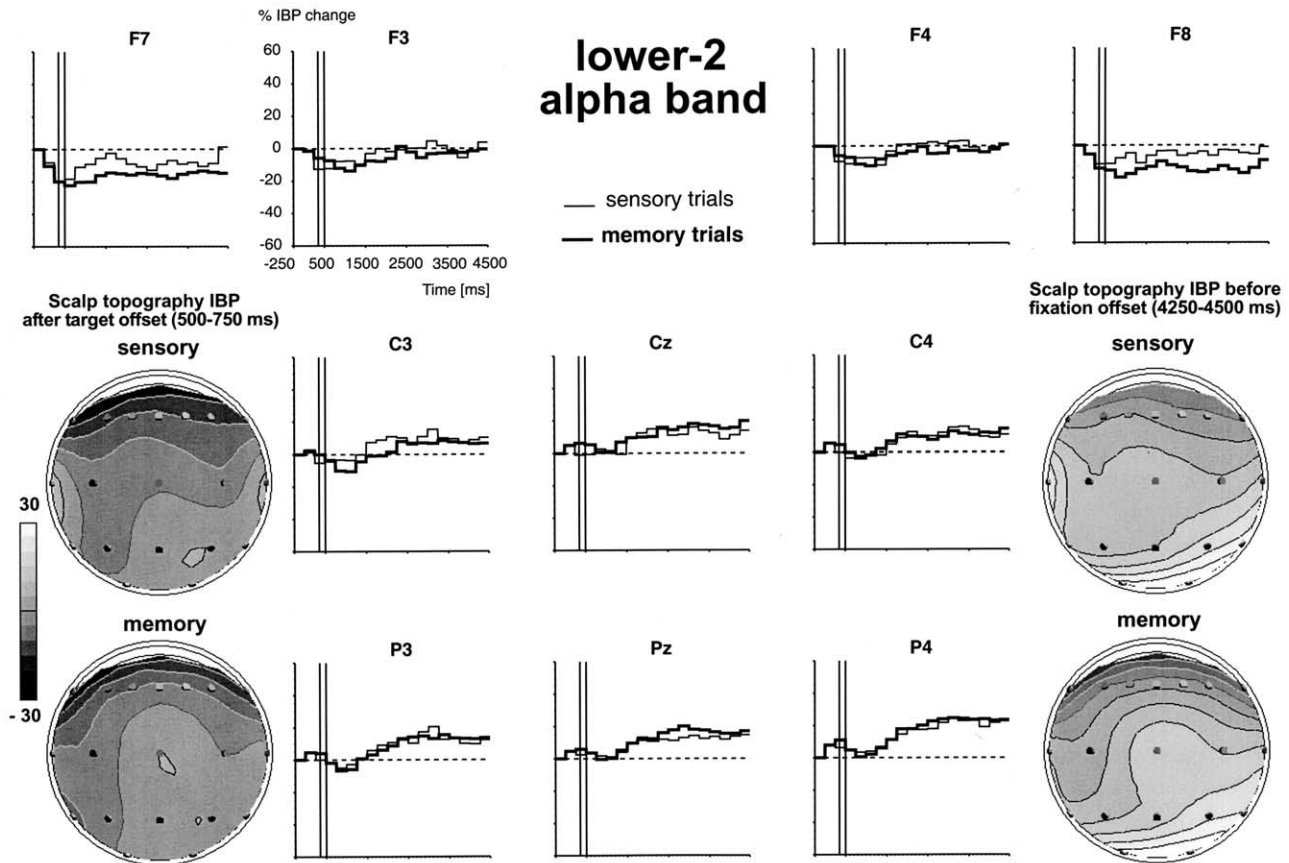
Fig. 4. Time courses at selected electrodes, and topographic maps at selected time points, of the percent induced band power (IBP) changes in the lower-2 alpha frequency band in the S4 and M4 conditions. See Fig. 2 for further details.

fore, effects occurring in the theta and lower-1 alpha bands in the present study may be interpreted to be specific to the theta frequency range, while effects occurring in the lower-2 and upper alpha bands in the present study may be interpreted to be specific to the alpha frequency range. In the remainder of this paper, we will therefore distinguish between the theta band (pooling over theta and lower-1 alpha bands) and the alpha band (pooling over the lower-2 and upper alpha bands), rather than between the 4 narrow frequency bands used so far.

The phasic IBP increase in the theta band, which immediately follows the presentation of the target stimulus is clearly a task-related effect, in the sense that it occurs regardless of condition or retention interval. The effect is small, and could possibly have gone unnoticed if a more common number of subjects (i.e. 10 or 20) would have been used. Nonetheless, the effect is highly similar to the well-established pattern of results generally obtained by Klimesch and coworkers (e.g. Klimesch, 1999), of a theta increase in tasks which engage encoding and retrieval of episodic information. Therefore, this effect may reflect the process of encoding the location of the target stimulus. Such an interpretation is further supported by the scalp distribution of the effect (see the topographic maps in Figs. 2 and 3): irrespective of condition, it is maximal over parietal areas,

which corresponds to the dorsal visual pathway generally associated with locating objects in space.

The sustained IBP increase over posterior electrodes in the alpha band is clearly task-related, since both the time courses and the scalp distributions are identical for the memory and the sensory conditions. The effect could be related to reduced activity in loops involving thalamus and visual cortex, reflecting reduced activity of the visual system. A number of arguments are in favor of such an interpretation: First, neurobiological research has suggested that enhanced alpha activity is indicative of cortical idling (cf. Steriade et al., 1990; Lopes da Silva, 1991; Guillery et al., 1998). Second, the alpha enhancement in the present study has an occipito-parietal maximum which is most prominent at the end of the retention interval (see the topographical maps at the right-hand side of Figs. 4 and 5). This is consistent with findings indicating that the scalp topography of alpha reactivity is dependent on the sensory modality of an attended stimulus (e.g. Bastiaansen et al., 2001), with larger alpha amplitudes being present over the sensory cortex of the unattended modality (Foxe et al., 1998). Therefore, it seems reasonable to relate the IBP increase over posterior electrodes in the higher frequency bands to reduced attention to or reduced processing of stimuli in the visual modality during the retention interval. This
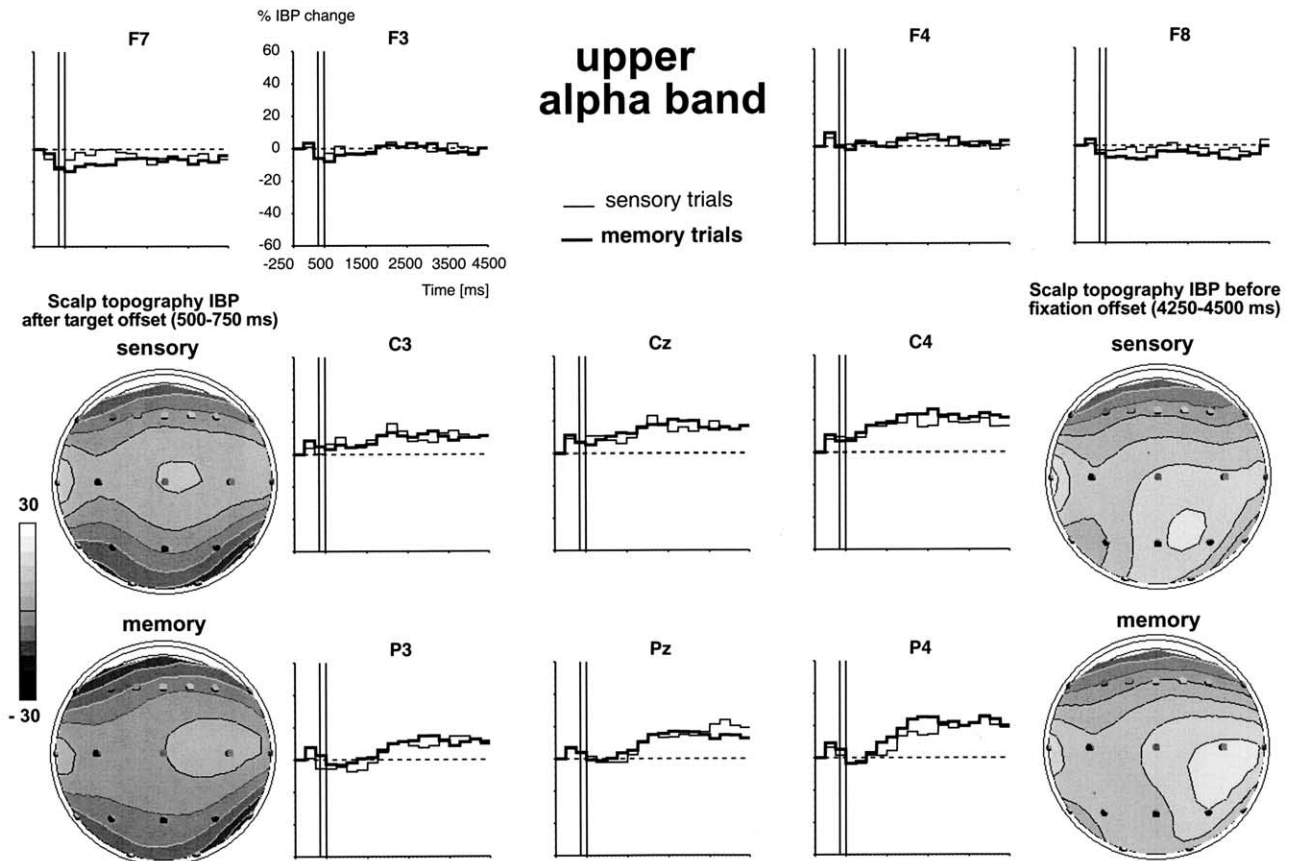
Fig. 5. Time courses at selected electrodes, and topographic maps at selected time points, of the percent induced band power (IBP) changes in the upper alpha frequency band in the S4 and M4 conditions. See Fig. 2 for further details.

would serve the role of inhibiting the processing of sensory stimuli, which would interfere with the retention of the target location in WM.

The most important finding of the present paper is the sustained decrease in IBP at anterior electrodes that is significantly larger in memory trials compared to sensory trials. Because it is found in both sensory and memory conditions, this decrease in theta IBP is considered to be a task-related effect. The effect appears to start prior to the target stimulus. Therefore, it may be argued that it is related to anticipatory processes. However, we feel that this is not likely to be the case for 3 reasons. First, anticipatory attention to an upcoming stimulus mainly results in power decreases in higher frequency bands (mainly 8–10 and/or 10–12 Hz bands; Bastiaansen et al., 1999, 2001; Pfurtscheller, 1992; Pfurtscheller and Klimesch, 1991). This is at odds with the present effect, which is present roughly in the 4–8 Hz frequency band. Second, if the anticipated stimulus is presented in the visual modality, the power decreases are usually maximal over the occipital areas (same references as before), whereas the present effect has a lateral frontal maximum. And third, the present effect is sustained, and even increases in strength, throughout the entire delay period, lasts 4 s. We feel that it is more likely that the early, i.e. pre-target onset of this effect results from the poor temporal

resolution of the IBP analysis method (see Knösche and Bastiaansen, 2002 for an elaborate discussion of the temporal resolution of IBP analysis).

A parsimonious interpretation of this effect is that both sensory and memory conditions engage visuo-spatial WM processes, but that these are engaged to a larger extent in the memory condition. How do these findings relate to underlying neurophysiological processes? Elsewhere, we have extensively discussed the hypothesis that theta reactivity is related to changes in activity in cortico-hippocampal loops (Bastiaansen and Hagoort, 2001). We will shortly address this hypothesis, and apply it to theta reactivity as measured here.

The hippocampus, a structure known to be involved in mnemonic processes (e.g. Squire and Zola-Morgan, 1991), generates oscillatory activity in the theta frequency range (e.g. Green and Arduini, 1954; Petsche et al., 1962). Therefore, it seems reasonable to assume that the hippocampal theta rhythm may be important for a variety of mnemonic functions. Additional evidence for this point of view stems from the apparent relation between theta and long-term potentiation (LTP; Larson et al., 1986; Arai and Lynch, 1992), and from the observation that disrupting the hippocampal theta rhythm produces memory deficits that are similar to hippocampal lesions (e.g. Winson, 1978).

Table 1
Significant ($P < 0.01$) main and interaction effects of the omnibus ANOVAs on the percent IBP changes[a]

| Effect | $F$ | df | $P$ |
|---|---|---|---|
| **Analysis I (1st second)** | | | |
| Theta band | | | |
| Condition | 11.25 | 1, 170 | 0.001 |
| Anteriority | 63.07 | 1, 170 | < 0.001 |
| Anteriority × Epoch | 4.34 | 2.00, 339.67 | 0.014* |
| Lower-1 alpha band | | | |
| Condition | 17.52 | 1, 170 | < 0.001 |
| Anteriority | 18.18 | 1, 170 | < 0.001 |
| Anteriority × Epoch | 5.57 | 2.34, 398.19 | 0.002 |
| Anteriority × hemisphere | 8.47 | 1, 170 | 0.004 |
| Lower-2 alpha band | | | |
| None | | | |
| Upper alpha band | | | |
| None | | | |
| **Analysis II (entire delay)** | | | |
| Theta band | | | |
| Condition | 13.61 | 1, 170 | < 0.001 |
| Anteriority | 64.77 | 1, 170 | < 0.001 |
| Second | 4.90 | 2.74, 465.36 | 0.003 |
| Lower-1 alpha band | | | |
| Condition | 8.46 | 1, 170 | 0.004 |
| Anteriority | 10.74 | 1, 170 | < 0.001 |
| Lower-2 alpha band | | | |
| Second | 10.76 | 2.04, 346.48 | < 0.001 |
| Upper alpha band | | | |
| Second | 6.01 | 2.06, 349.62 | 0.002 |
| Anteriority × Second | 4.92 | 2.25, 382.17 | 0.006 |

[a] Only effects involving within-subjects factors are listed. Greenhouse–Geisser-corrected degrees of freedom and *P*-values are given. *, marginally significant.

Although both the position and the closed-field structure of the hippocampus make it unlikely that the electrical activity generated in this structure is detected in the scalp-recorded EEG, it has been suggested that hippocampal theta may be transferred to the cortex through hippocampo-cortical pathways (Miller, 1991; Treves and Rolls, 1994). On the basis of anatomical and computational arguments, Treves and Rolls (1994) proposed a theory of episodic memory, in which the hippocampus stores memories of contiguous events which can be evoked when a fraction of the episode is available as a cue. When this occurs, the hippocampus would reinstate the entire memory by reactivating those parts of the cortex that were active at the time the memory trace was initially formed. If this cortical reactivation takes place at the dominant frequency of the hippocampus, it can be detected with scalp electrodes. Put differently, theta activity in the scalp-recorded EEG could provide a window on cortico-hippocampal interplay by measuring activity at the cortical end of the loop.

If one is willing, for a moment, to assume that scalp-recorded activity in the theta frequency range is indeed generated by (para)hippocampo-cortical circuits, then the logical consequence is that a power increase reflects enhanced activity, while a power decrease is a reflection of a reduced activity in these circuits. Applying these ideas to the present data, the phasic theta power increase after the presentation of targets reflects an increase in activity in hippocampal–parietal circuits, corresponding to the encoding of the target location. The sustained power decrease at anterior sites during the entire retention interval can be ascribed a functional role in enhancing the signal-to-noise ratio of the activity in the hippocampo-parietal loop involved in encoding (and possibly maintaining) the location of the target stimulus, by reducing the noise (i.e. the activity in other hippocampo-cortical loops) relative to the signal (i.e. the activity in the hippocampo-parietal loop). An argument in favor of such an interpretation is that irrespective of condition, the scalp topography of the IBP in the theta and lower-1 alpha bands shows maximal power in these frequency bands at parietal electrodes throughout the entire WM interval (see topographical maps in Figs. 2 and 3), whereas the main difference between sensory and memory conditions is the power reduction at other scalp locations. This interpretation implies that the dorsolateral prefrontal cortex, known as the locus of executive WM functions (e.g. Frisk and Milner, 1990; Owen et al., 1996; Goldman-Rakic, 1996), plays an active role in suppressing (inhibiting) activity in irrelevant hippocampo-cortical loops.

However, it is questionable whether scalp-recorded theta activity is generated *exclusively* in the (para)hippocampo-cortical feedback circuits. Other mechanisms or network dynamics may also be involved in the theta reactivity observed in the present study. For example, Von Stein and Sarnthein (2000) have proposed that increases in theta coherence may be indicative of interactions between cortical areas that are spatially distant from each other. More specifically, these authors hypothesize that "cortico-cortical interactions between prefrontal and posterior cortex during WM retention evolve with a temporal dynamics in a low frequency range (theta, 4–8 Hz)" (Von Stein and Sarnthein, 2000, p. 308). In sum, we feel that although a 'signal-to-noise ratio enhancement' interpretation of the effects in the theta band is attractive in the sense that it would fairly well account for the pattern of results obtained in this study, we have insufficient empirical data to exclude other explanations. Full understanding of the neurophysiology underlying

Table 2
Differences between memory and sensory conditions in the lower frequency bands, for both analyses[a]

| | | Theta | Lower-1 alpha |
|---|---|---|---|
| Analysis I | Sensory | −5.3 (3.2) | −1.6 (2.9) |
| | Memory | −14.5 (2.5) | −11.6 (2.1) |
| Analysis II | Sensory | −7.8 (3.5) | 1.5 (3.6) |
| | Memory | −19.4 (2.8) | −7.9 (2.9) |

[a] Figures given are mean (standard error) percentage IBP change, where negative percentages indicate a power decrease, while positive percentages indicate a power increase.

the present WM effect clearly must await further experimentation.

We have investigated for the first time the event-related changes in alpha and theta power in relation to visuo-spatial WM. Most interestingly, the theta decrease that we find to be related to visuo-spatial WM stands in sharp contrast with the increases that have been reported during other forms of memory – i.e. episodic encoding and retrieval (Klimesch, 1999) and verbal WM (Krause et al., 2000). Therefore, this study testifies to the high degree of sensitivity of the IBP changes in the theta and alpha frequency bands to different aspects of human memory performance. In the present data, we found a significant dissociation between memory encoding (phasic theta increase, parietal) and visuo-spatial WM (tonic theta decrease, anterior). More generally, while encoding and retrieving information from (episodic) memory induces a phasic increase in theta power in a very narrow frequency band (that is, 4–6 Hz if the average individual alpha peak (IAF) of subjects lies around 10 Hz, e.g. Klimesch, 1999), activation of WM in a task employing linguistic material leads to increases in band power in the 6–10 Hz frequency bands which varies with WM load (Krause et al., 2000), and activation of visuo-spatial WM is accompanied by a sustained decrease in theta power in the 4–8 Hz frequency band (if the average IAF of subjects is 10 Hz, present data). These differential patterns of results obtained with respect to theta and alpha band reactivity indicate that the brain honors the theoretical distinctions between episodic memory, and domain-specific components of WM, such as verbal WM and visuo-spatial WM.

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