

# EEG alpha distinguishes between cuneal and precuneal activation in working memory

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In the literature on EEG during working memory (WM), the role of alpha power (8–13 Hz) during WM retention has remained unclear.

We recorded EEG while 18 subjects retained sets of consonants in memory for 3 s; setsize (ss4, ss6, ss8) determines memory workload.

Theta power (4–8 Hz) increased with workload in all subjects in middle frontal electrodes. Using ICA, the increase in theta could be attributed to one component whose generators were localized by sLORETA in the medial frontal gyrus.

Alpha power in parietal electrode Pz showed a mean increase during retention as compared to prestimulus fixation (event-related synchronization, ERS). On an individual basis, alpha power increased with workload in 9 subjects (WL+ group) and decreased in 9 subjects (WL– group). The alpha increased in upper alpha for the WL+ group (mean: 10.4 Hz) and decreased in lower alpha for the WL– group (mean: 8.9 Hz). Time–frequency representations show high alpha power early during retention for the WL+ group and high alpha power late during retention for the WL– group. sLORETA revealed maximal contrast for the WL+ group in the cuneus and for the WL– group in the precuneus.

In subjects with WL+, alpha increase in the cuneus may reflect WM maintenance or active inhibition of task-irrelevant areas. In subjects with WL–, alpha decrease in the precuneus may reflect release of inhibition associated with attentional demands. Thus, alpha EEG characterizes two aspects of processing in the same WM task.

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**Keywords:** Theta; Attention; Prefrontal cortex; ICA; sLORETA

**Abbreviations:** BA, Brodmann area; EEG, electroencephalogram; ERD, event-related desynchronization; ERS, event-related synchronization; ERSP, event-related spectral perturbation; FFT, fast Fourier transform; IC, independent component; ICA, independent component analysis; sLORETA, standardized low resolution brain electromagnetic tomography; ss, setsize; WM, working memory.

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## Introduction

Working memory (WM) is defined as our capacity to keep information actively “in mind” for short periods of time as this information is used to guide behavior. In line with the finding of hippocampal theta oscillations in animals, it has been proposed that oscillatory brain activity is essential for sustaining WM representations also in humans (Lisman and Idiart, 1995; Buzsaki, 2006). While oscillations in several frequency bands are affected by WM processes, their functional role is still debated.

Several authors have reported an increase in frontal theta power with memory workload for a large variety of WM tasks (Gevins et al., 1997; Klimesch, 1999; Krause et al., 2000; Kahana et al., 2001; McEvoy et al., 2001; Raghavachari et al., 2001; Fingelkurts et al., 2002; Jensen and Tesche, 2002; Onton et al., 2005). But also for many subjects the absence of frontal theta power increase has been reported (e.g. Jensen et al., 2002).

The concurrent association of WM activity with changes in alpha power has ignited a vivid debate on the role of alpha in memory processing. In particular, the role of alpha between WM activity (Jensen et al., 2002; Jokisch and Jensen, 2007; Tuladhar et al., 2007), cortical idling (Pfurtscheller et al., 1996), attention (Klimesch et al., 1999) and top–down processes in general (von Stein et al., 2000; von Stein and Sarnthein, 2000) is being discussed (Klimesch et al., 2007; Palva and Palva, 2007). Usually, an increase of alpha power with respect to baseline is called event-related synchronization (alpha ERS) and a decrease event-related desynchronization (alpha ERD). It has been proposed that alpha ERS plays an active role for the inhibitory control of cortical processing whereas alpha ERD reflects the gradual release of inhibition associated with complex activation processes (Klimesch et al., 2007).

In order to solve a WM task, attention is one of the complex activation processes required. For example, memory retrieval might reflect a form of selective attention to internal representations (Badre et al., 2005; Wagner et al., 2005). Therefore, both attention-related and memory-related processes should occur during WM retention. Since different subjects may well use different brain processes to solve the same task, we hypothesized

that attention-related and memory-related processes may appear in different subjects to different extent and that this extent may be observable in the EEG.

To describe the modulatory effects of WM activity on both theta and alpha, we selected 18 subjects with a marked workload dependence of theta power. In the alpha band, the analysis of spectral power, time–frequency representation and the localization of cortical EEG generators revealed a distinction between the subjects in two subgroups. In one subgroup, alpha increase with workload in the cuneus could reflect WM maintenance or active inhibitory control of task-irrelevant areas. In the other subgroup, alpha decrease with workload in the precuneus may reflect the release of inhibition associated with attentional demands.

## Materials and methods

### Subjects

We recorded the EEG from a total of 23 subjects aged 19–50 years. Of these, we selected those subjects whose frontal theta power increased with memory workload and ICA converged to a single frontal component. The final sample consisted of 18 subjects (six women and 12 men) with a mean age of 32.8 years  $\pm$  7.4 years. The study was approved by the Kanton Zürich ethics committee. All subjects were informed about the aim and the scope of the study and gave written informed consent according to the declaration of Helsinki. All subjects had vision normal or corrected to normal and were screened for health problems using a detailed health questionnaire. The subjects had no current or previous history of relevant physical illness and they were not currently taking drugs or medication known to affect their EEG.

### Experimental design

We used a modified Sternberg task where encoding of memory items, retention and recall are temporally separated, Fig. 1A (Jensen et al., 2002). Each trial started with the word “Blink”, encouraging the subjects to make eye blinks in order to reduce artifacts later in the trial. After the subjects triggered the advancement of the trial by button press, a fixation dot was presented for 1 s (fix). After that, a set of consonants (stimulus) was presented at the center of the screen for 2 s and had to be retained in memory for 3 s. All stimuli contained eight consonants. Of these the middle four, six or eight letters were the memory items. In case of memory setsize (ss) four (ss4) and six (ss6) the outer positions were filled with ‘X’ which was never a memory item. Thus, the physical size and the visual content of the stimulus were the same, irrespective of the size of the memory set. During both stimulus presentation and retention interval a fixation dot was presented at the center of the screen.

After the retention interval, a probe letter replaced the fixation dot. Subjects indicated whether the probe was part of the stimulus by button press on a joystick (‘yes/no’ procedure). Subjects had been instructed that correct response was more important than short reaction time. After the response, the probe was turned off and subjects received acoustic feedback whether their response was correct or incorrect. Trials with different ss were presented in random order except after an error, which was always followed by a trial with ss4. Because there was no significant difference in our results for correct ‘yes’ and correct ‘no’ trials, data were pooled across these trial types. Although stimuli are presented visually in

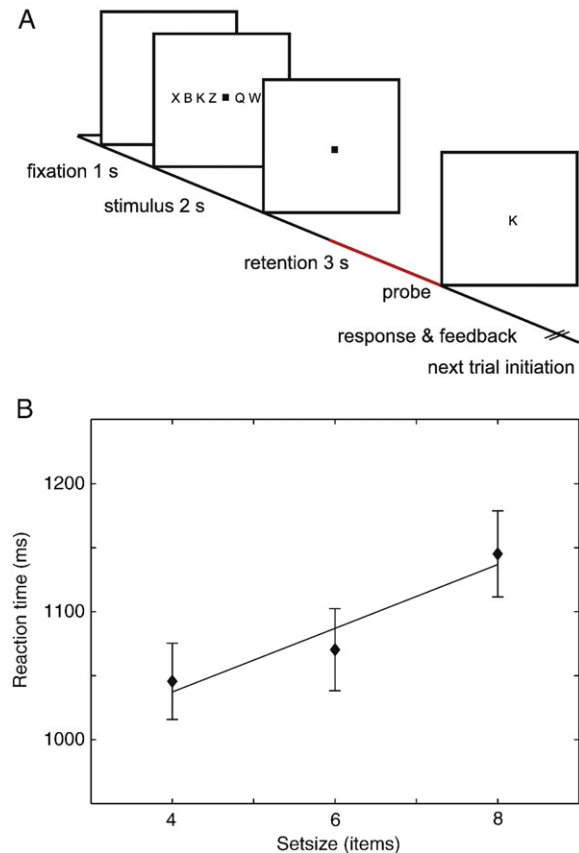


Fig. 1. Behavioral experiment. (A) In the task, sets of consonants (stimulus) had to be retained in memory for 3 s. The setsize (4, 6, or 8 letters) determines the memory workload. For ss4 and ss6, four and two positions on the screen were filled with the letter ‘X’ to keep the number of letters constant on the screen. After the retention interval a probe letter was shown. Analysis focused on the last 2 s of the retention interval (red line). Subjects were asked to decide whether the probe was part of the stimulus by pressing a button on a joystick. (B) Reaction times increased systematically with a slope of 28 ms/item.

this task, letter strings are thought to activate the phonological loop during the retention interval (Baddeley, 2003).

### EEG recording sessions

Subjects were seated in a dimly lit room shielded against sound and stray electric fields and were video monitored. The recording sessions were performed between 9 and 12 h in order to exclude an impact of circadian factors on the EEG. Subjects were advised to abstain from caffeinated beverages on the day of recording to avoid the caffeine-induced theta decrease in the EEG (Landolt et al., 2004). Before each recording, subjects were instructed to assume a comfortable position in a chair and were free to place their head on a chin-rest.

EEG signals were measured with 60 Ag/AgCl surface electrodes, which were fixed in a cap at the standard positions according to the extended 10–10 system (M11, Easycap, Herrsching, Germany). During recording, electrode CPz served as reference. Impedance was below 5 k $\Omega$  in all electrodes processed in further analysis. Additionally, two bipolar electrode channels were used to monitor eye movements. EEG signals were registered using the SynAmps EEG system (Neuroscan Compumedics, Houston, TX, 0.017 nV

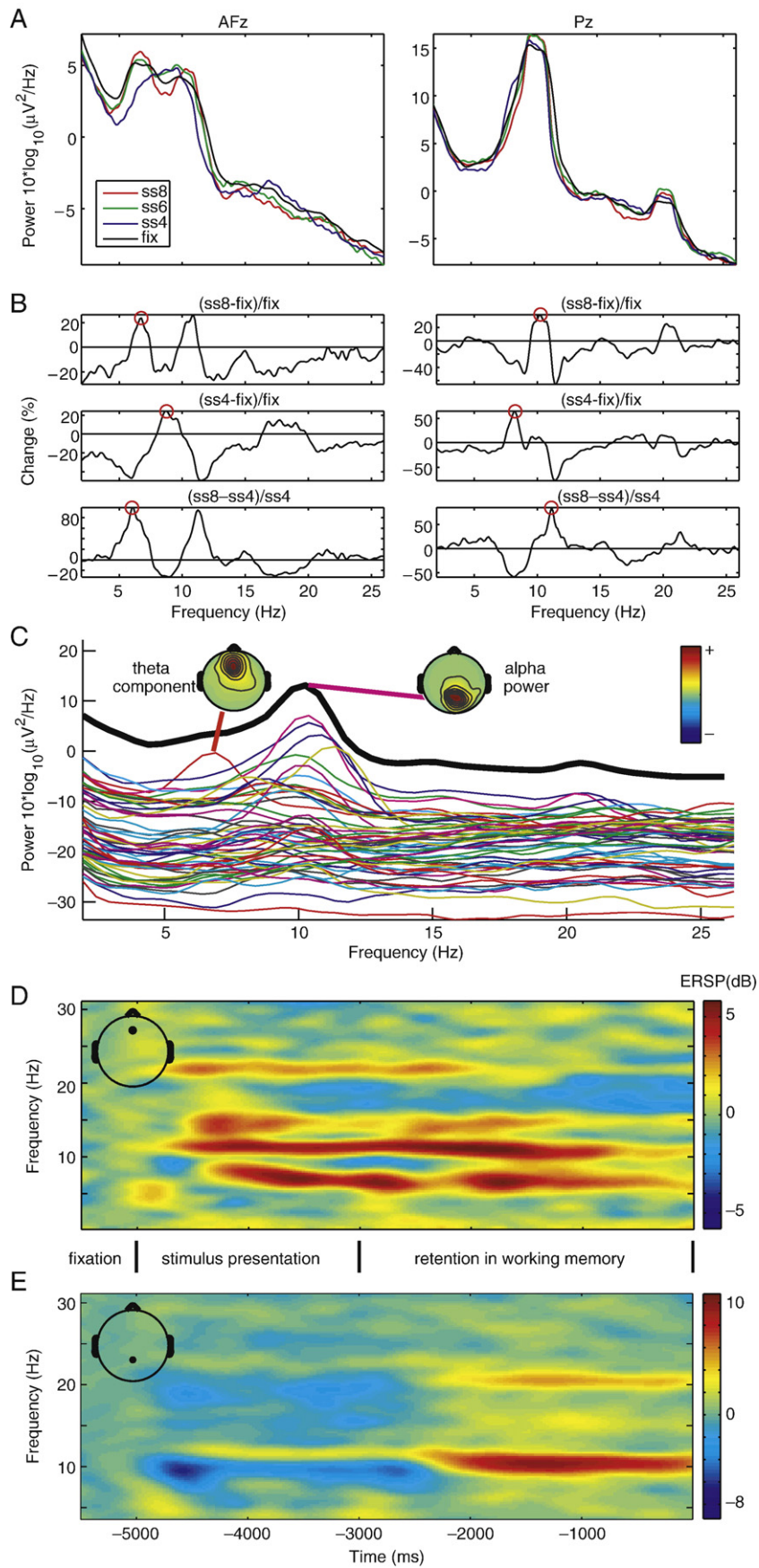


Table 1  
Spectral parameters for individual subjects

Subject	AFz		Variance explained by $\theta$ IC			Pz		sLORETA					
	Theta (4–8 Hz)		ss8 (%)	ss6 (%)	ss4 (%)	Alpha (8–13 Hz)		ss8 (dB/sec)	ss4 (dB/sec)	Alpha (8–13 Hz)			
	(ss8–ss4)/ss4					(ss8–fix)/fix	(ss4–fix)/fix			(ss8–ss4)/ss4	dP $\alpha$ /dt	dP $\alpha$ /dt	Location of max
	Height (%)	Frequency (Hz)				Height (%)	Height (%)			Height (%)	Frequency (%)	ss8	
1	99	6.0	41.5	33.9	21.9	39	64.6	86	11.1	-2.1	-1.0	BA 7	
2	51	7.0	54	48.5	38	-50	-50.4	40	11.9	-2.0	0.8	BA 18	
3	25	5.3	27.5	29.1	18.9	138	41.6	76	10.1	2.0	0.4	BA 7	
4	107	5.8	45.7	20.8	20.1	31	61.0	25	12.0	2.0	1.2	BA 18	
5	31	4.4	23.7	22.5	16	63	58.2	53	9.3	-0.9	0.8	BA 18	
6	18	4.3	45	30	22.4	42	20.2	48	10.8	-0.5	-0.4	BA 19	
7	52	6.8	59.1	72.2	48.1	-12	-17.2	30	9.3	-4.5	-3.0	BA 18	
8	33	5.3	48.9	49.5	26.1	3	11.6	34	10.5	-0.8	-2.0	BA 36	
9	44	6.1	70.7	61	52.6	-20	-21.6	9	9.1	-0.1	0.6	BA 18	
10	34	5.1	21.9	16.3	12.9	15	31.4	-32	8.5	2.9	1.1	BA 18/19	
11	60	5.6	22.9	11.6	5.8	54	73.9	-29	8.0	1.3	0.5	BA 7	
12	79	5.5	19.2	15.6	5.6	12	69.8	-47	9.5	0.8	0.5	BA 7	
13	11	7.3	17.3	15.3	13.3	-34	-2.2	-38	8.9	-0.2	-2.8	BA 17	
14	13	5.0	69.3	64.8	33	65	122.3	-41	9.4	2.8	2.9	BA 7	
15	12	7.5	28.6	22.8	24.7	-32	68.1	-68	10.1	0.7	0.4	BA 7	
16	48	5.6	43.3	39.5	29.3	-15	42.0	-62	10.0	1.5	-1.9	BA 7	
17	1	4.4	17	17.4	11.7	17	169.5	-67	8.0	0.0	0.8	BA 4	
18	68	4.4	32.3	38.3	10.3	14	37.4	-54	8.0	1.8	1.0	BA 7	
Mean of all subjects	43.7	5.6	38.2	33.8	22.8	18.3	43.3	-2	9.7	0.3	0.0	BA 18	
$r^2$	0.14	0.02	0.06	0.01	0.07	0.08	0.18	0.89	0.46	0.18	0.01		
Mean of subjects 1–9 (WL+ group)	51.2	5.6	46.2	40.8	29.3	26.0	18.7	45	10.4	-0.8	-0.3	BA 18/19	
Mean of subjects 10–18 (WL- group)	36.2	5.6	30.2	26.8	16.3	10.6	68.0	-49	8.9	1.3	0.3	BA 7	
$p$ (WL+ group vs. WL- group)	0.387	0.285	0.024	0.077	0.040	0.6665	0.040	0.000	0.011	0.024	0.436		

Frontal electrode AFz shows an increase in the theta band for all subjects. For the  $\theta$ IC, the variance explained is higher for ss8 than ss4 in all subjects. In parietal electrode Pz, the mean of all subjects shows ERS for ss8 and ss4; subjects of the WL+ group show higher ERS for ss8 and subjects of the WL- group show higher ERS for ss4 (Fig. 4). In the workload dependence, subjects 1–9 show alpha increase (WL+ group) and subjects 10–18 show alpha decrease (WL- group). Subjects are ordered with respect to workload dependence in alpha, leading to a high coefficient of regression of this observable with subject number ( $r^2=0.88$ ). Group-wise comparison of spectral parameters used non-parametric Wilcoxon tests. ERS peak frequencies for the WL+ group in the alpha band were significantly higher than the ERS peak activations for the WL- group. The slope  $dP\alpha/dt$  indicates the direction of power change during the 2 s retention interval. In 7/9 subjects of the WL+ group spectral power was low at the end of the retention interval (negative slope), whereas the spectral power was high at the end of the retention interval in 7/9 subjects of the WL- group (positive slope). The location of maximal sLORETA activation for ss8 was located predominantly in cuneal Brodmann areas (BA) in subjects of the WL+ group and in precuneal areas in subjects of the WL- group.

precision, sampling rate 250 Hz, 0.3–100 Hz analog band pass filter, -12 dB/octave) and continuously viewed on PC monitor.

#### Data preprocessing and editing

Data were analyzed offline in Matlab (The Mathworks, Natick, MA) using EEGLAB (<http://scn.ucsd.edu/eeglab/index.html>) (Delorme and Makeig, 2004) and custom scripts. First, the scalp

EEG was re-referenced to the mean of the signals recorded at the ear lobes. Data were then high-pass filtered with a filter of 0.5 Hz to remove linear trends that would negatively affect the independent component analysis (ICA). Only correct trials were used for the analysis. We focused on the last 2 s of the retention interval to avoid interference from visual evoked responses and eye blink artefact. Data were inspected visually and eye movement, muscles or heart beat artifacts were removed. The EEG was

Fig. 2. Spectral analysis in subject 1. (A) Workload dependence of spectral power at frontal electrode AFz (left) and electrode Pz (right) for the three setsizes (ss) and prestimulus fixation (fix). The largest effect at AFz appears around 6 Hz in the theta band. (B) Event-related synchronization (ERS) for ss8 (top panels) and ss4 (middle panels). For workload dependence, trials with ss4 were used as baseline (bottom panels). The workload dependence at AFz shows two maxima, one at 6.1 Hz in the theta band and one at 11.1 Hz in the alpha band. (C) Spectral power for ss8. The single frontal IC is maximal at frontal electrodes at 6.8 Hz ( $\theta$ IC). The mean alpha power (~10 Hz) is maximal at parietal electrodes. (D) Event-related spectral perturbation (ERSP) for ss8 at electrode AFz. The prestimulus fixation interval between -6000 and -5000 was taken as baseline. The time window -5000 ms to -3000 ms shows the stimulus period followed by the retention interval from -3000 ms to 0 ms. (E) ERSP for ss8 at electrode Pz. After a period of low alpha power in the beginning of the retention interval, alpha increased around -2000 ms. Alpha power decreased towards the end of the retention interval.

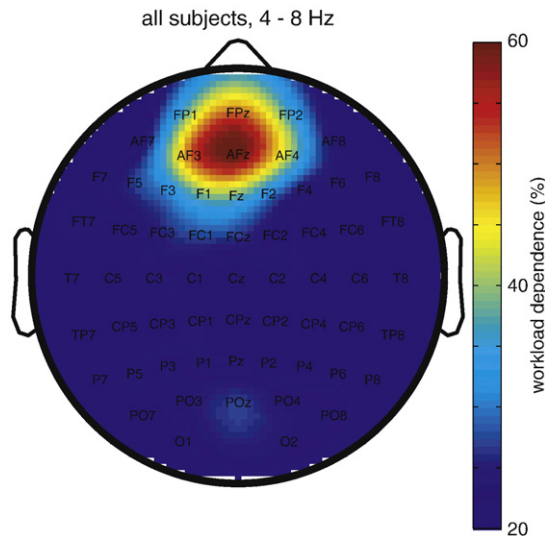


Fig. 3. Topography of workload dependence of theta power. The median increase across all subjects is maximal at frontal electrode AFz.

decomposed into independent components using ICA blind separation. After removal of artifact components the signal was reconstructed. Since ICA has proved capable of separating biologically plausible brain sources whose brain activity patterns are distinctly linked to behavioral phenomena (Makeig et al., 1999; Jung et al., 2000), we also analyzed independent components (ICs) for each individual subject.

#### Power spectral density

The spectral analysis was performed with the multitaper method, which provides a formal method to obtain estimates from the spectrum with optimal bias and variance properties (Mitra and Pesaran, 1999) (<http://www.chronux.org>). Spectra were calculated with a window length of 2 s, fast Fourier transform (FFT) length of 8 s, and bandwidth parameter  $nw=2$  and  $k=3$  tapers (Percival and Walden, 1993). Spectral peaks were determined, and the peak position was classified with respect to the frequency bands: theta (4–8 Hz), alpha (8–13 Hz), beta (13–30 Hz).

#### Event-related power

The power in trials with ss8 or ss4 was compared to the power of the prestimulus fixation interval for each frequency point according to:

$$\text{Event-related power} = (\text{power}_{\text{ss8}} - \text{power}_{\text{fix}}) / \text{power}_{\text{fix}} * 100$$

We determined the extremes of the event-related power for theta and alpha bands. Positive values denote event-related synchronization (ERS) and negative values denote event-related desynchronization (ERD) (Pfurtscheller and Aranibar, 1977).

#### Workload dependence

The power in trials with ss8 was compared to trials with ss4 for each frequency point according to:

$$\text{Workload dependence} = (\text{power}_{\text{ss8}} - \text{power}_{\text{ss4}}) / \text{power}_{\text{ss4}} * 100$$

We determined the extremes of the workload dependence for theta and alpha bands. Taking ss4 trials as a baseline has the advantage that the task condition (ss8) and the baseline condition (ss4) were recorded under the same circumstances and only the WM workload differed between the two conditions.

#### Event-related spectral perturbation (ERSP)

Each single trial EEG time series was transformed to a spectrographic image using short sliding time windows. The prestimulus fixation interval was taken as baseline. Subtracting the baseline from log power at each frequency and trial gave single-trial ERSP images (Makeig, 1993). Each of these spectral transforms of individual response epochs was then normalized by dividing by their respective mean baseline spectra. Normalized response transforms were averaged to produce the average ERSP.

#### Source analysis

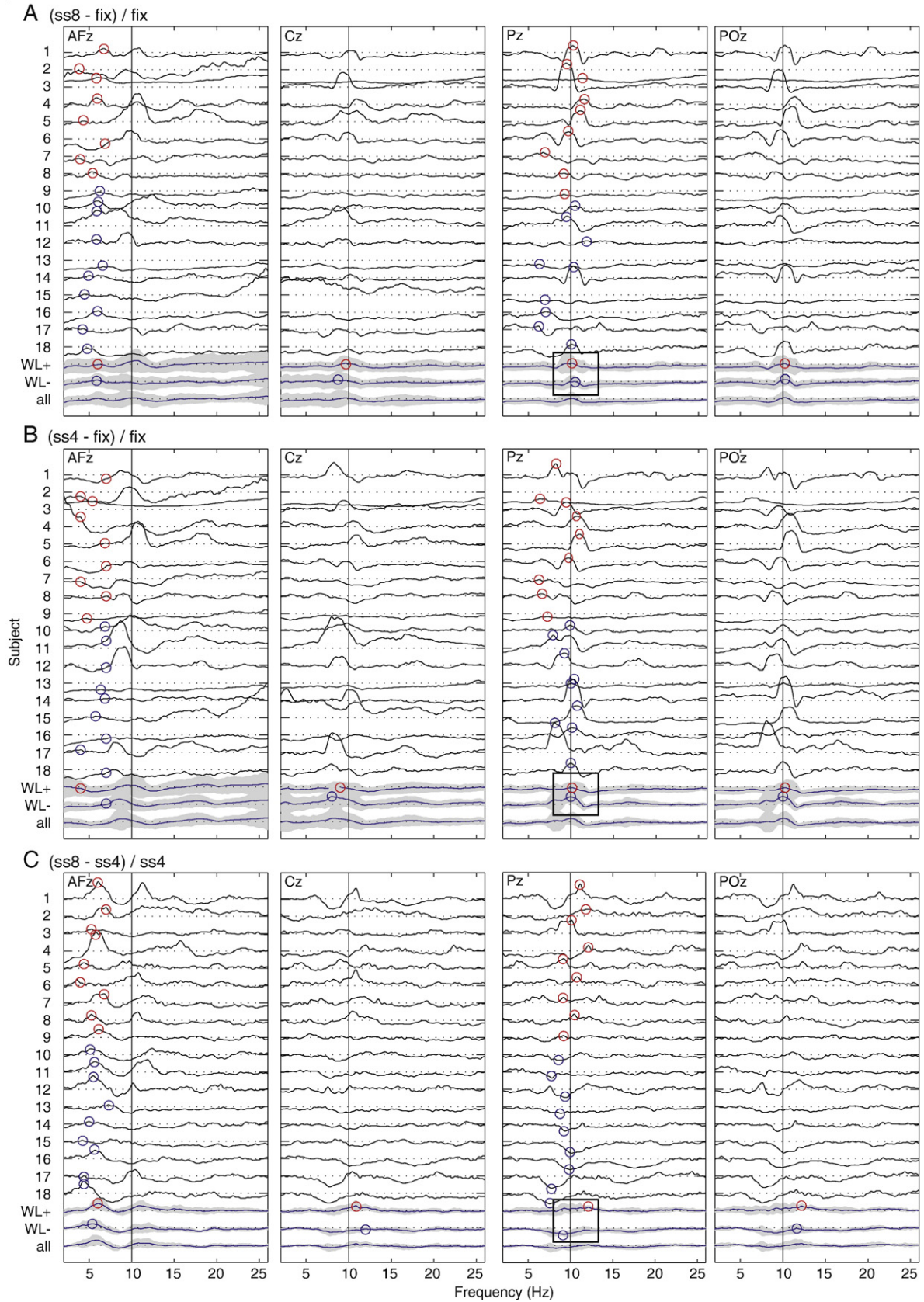
We used standardized low resolution brain electromagnetic tomography (sLORETA) to localize the generators of the scalp EEG power spectra. The sLORETA solution space is restricted to the cortical gray matter in the digitized MNI atlas with a total of 6239 voxels at 5 mm spatial resolution (Pascual-Marqui et al., 2002). We calculated tomographic sLORETA images corresponding to the estimated neuronal generators of brain activity within a given frequency range (Frei et al., 2001). A spatial over-smoothing with signal-to-noise ratio 10 was chosen for the sLORETA transformation matrix. This procedure resulted in one 3D LORETA image for each subject and ss for a given frequency range. sLORETA statistical contrast maps were calculated through multiple voxel-by-voxel comparisons in a nonparametric test for functional brain imaging (Nichols and Holmes, 2002) with smoothing 1 and linear scaling. The significance threshold was based on a permutation test with 5000 permutations. The  $t$ -values were plotted onto a MRI template with a scale bar indicating statistical power and color scale exponent equal to five. Results are presented both in anatomical coordinates and in Brodmann areas (BA).

## Results

#### Behavioral results

The behavioral data were analyzed in terms of reaction times and correct responses. The correct response rate across all subjects and all ss was  $91.9 \pm 6.6\%$ . For ss8, the mean correct response rate was  $85 \pm 5\%$ . Subjects achieved an average of 145, 115, and 103 correct trials for ss4, ss6, and ss8 respectively. The mean response

Fig. 4. Spectra of ERS and workload dependence for midline electrodes AFz, Cz, Pz and POz. In alpha at Pz, subjects of the WL+ group show higher ERS for ss8 (A) and subjects of the WL- group show higher ERS for ss4 (B). Maxima are circled in theta at AFz and in alpha at Pz. The dotted line indicates zero. (C) Spectra of workload dependence (ss8–ss4)/ss4 for all subjects. In theta at AFz, all subjects show positive workload dependence. At Pz, extremes in the alpha band are circled. Subjects 1–9 show alpha increase (red circles maxima, WL+ group). Subjects 10–18 show alpha decrease (blue circles minima, WL- group). Group averages are shown with the standard deviation (shaded ribbon), which excludes zero for the two groups separately (box), but not for the grand average.



time systematically increased by 28 ms/item (Fig. 2B). The increase in response time with ss complies with the findings of the original Sternberg task (38 ms/item; Sternberg, 1966). Subjects reported that, in their effort to solve the task, they relied mainly on audioverbal transformation of the letters and chunking.

#### *Spectral analysis for subject 1*

##### *Spectral power*

At electrode AFz, we observed a gradual increase in spectral power for higher ss which was most visible in the theta band (Fig. 2A, left panel). This increase in power is reflected in theta ERS (Fig. 2B, top left panel) and also in the workload dependence (Fig. 2B, bottom left panel). In addition, the alpha power peak frequency was shifted for subject 1 (Fig. 2A, left panel), resulting in a high ERS in the alpha band for this frontal electrode. At electrode Pz, the power in the alpha band was stronger for ss8 than for fix and for ss4 as illustrated in Fig. 2A (right panel). This results in alpha ERS (Fig. 2B, top right panel). Also the workload dependence (Fig. 2B, bottom right panel) showed a positive extreme in the alpha band (86% at 11.1 Hz, Table 1).

##### *Independent component (IC)*

In component space, the ICA revealed one salient IC in the theta band during retention, which we refer to as  $\theta$ IC (Fig. 2C). While spectral power was also high in the alpha band, it was not attributable to a single IC. The  $\theta$ IC explains a different amount of variance in the EEG corresponding to ss8, ss6 and ss4. The variance explained by the  $\theta$ IC is maximal for ss8 and minimal for ss4 (Table 1). The workload dependence is evidence that this IC describes a brain process related to WM.

##### *Time–frequency representation*

The ERSP at electrode AFz shows both theta and alpha activation in this subject (Fig. 2D). At electrode Pz, alpha power during the retention interval was highly variable (Fig. 2E). The alpha ERSP was below baseline during retention until  $-2300$  ms, consistent with a recent finding with a visual WM task (Tuladhar et al., 2007). The maximum alpha ERSP around  $-1500$  ms was followed by a decrease towards the end of the retention interval.

#### *Spectral analysis for all subjects*

##### *Theta power*

At electrode AFz theta power increased with WM load in all subjects (Table 1, Fig. 4C). Over the group of subjects, the median theta increase was 43.7% at electrode AFz. Over all electrodes, the topography of median increase showed a frontal maximum at AFz (Fig. 3). A similar topography appeared also for all individual subjects.

##### *Contribution of $\theta$ IC*

The ICA decomposition of the EEG was characterized by a salient IC peaking in the theta band, as has been illustrated for subject 1 (Fig. 2C). The  $\theta$ IC did not appear in all 23 subjects who participated but was our criterion to select the final sample of 18 subjects. The variance of the EEG (ss8) which is explained by the  $\theta$ IC at its spectral maximum is listed in Table 1. To investigate whether this  $\theta$ IC was indeed related to WM load, we determined the amount of variance explained also for the EEG corresponding to lower WM load. The variance explained by the theta component was

minimal for ss4 in all subjects and increased monotonically with workload in 12 out of the 18 subjects (Table 1). One-way ANOVA showed that there was an interaction of ss and variance explained ( $F_{2,53}=4.17, p=0.02$ ). Post-hoc analysis revealed that the difference between ss8 and ss4 was significant ( $p=0.03$ ). Interestingly, the  $\theta$ IC explained more variance in the EEG of the subgroup of subjects 1–9 than in the EEG of the subgroup of subjects 10–18 (Table 1). This effect was significant for ss4 ( $p=0.040$ ) and ss8 ( $p=0.024$ ).

To identify the cortical generators of the theta activity, the weights of the  $\theta$ IC were back-projected for each subject to obtain the corresponding EEG for ss8 and ss4. From this EEG sLORETA activations were calculated in frequency space. A paired *t*-test across all subjects comparing sLORETA activations for ss8 and ss4 at the theta peak demonstrated a significant ( $p<0.01$ ) activation in the dorsal part of the medial frontal gyrus (BA 9, Fig. 8A).

##### *Alpha power*

Mean parietal alpha power increased with respect to prestimulus fixation over the group of all subjects (Table 1). This reproduces the original finding with this task (Jensen et al., 2002). Furthermore, alpha power gradually increased with memory workload in some subjects and decreased in others. A similar inter-individual variability has been reported for subjects performing WM tasks with digits (Meltzer et al., 2007). We calculated the spectral workload dependence at electrode Pz (Fig. 4C) and determined its extreme in the alpha band (Table 1). Based on the direction of the workload-dependent alpha change in individual subjects, two subgroups appear. One subgroup of nine subjects (1–9) is characterized by positive workload dependence due to higher alpha power for ss8 than ss4, which we will refer to as the *WL+* group. The other subgroup of nine subjects (10–18) showed lower alpha power for ss8 than for ss4 and will be referred to as *WL-* group. The variability over subjects in each group is low and the ribbon of standard deviation excludes zero, which is not the case for the grand average (Fig. 4C).

The workload dependence in alpha was strongest for parietal electrodes in both groups (Fig. 4C). Also the peak frequency of the spectral workload dependence differed for the two subgroups. The peak frequency for the *WL+* group ( $10.4\pm 1.1$  Hz, upper alpha) was significantly higher ( $p<0.01$ , Wilcoxon test) than the peak frequency for the *WL-* group ( $8.9\pm 0.9$  Hz, lower alpha) which is also reflected in the regression coefficient  $r^2=0.46$ . The difference in workload dependence is related to the finding that subjects of the *WL+* group showed higher ERS for ss8 and subjects of the *WL-* group showed higher ERS for ss4 (Table 1). Over scalp sites, the effects for alpha were strongest at Pz and decreased towards frontal and lateral electrodes (Fig. 5).

##### *Time–frequency representation*

During WM retention, parietal alpha power decreased towards the end of the retention interval in some subjects and increased in others. In Fig. 6A we show the mean ERSP of the whole trial during the highest WM workload (ss8) for the two groups. In the *WL+* group, ERSP at 10 Hz at electrode Pz was maximal between  $-2000$  to  $-1000$  ms and decreased in the last second of the retention interval. This time course reproduces the original finding for the same task (Jensen et al., 2002). For one member of the *WL+* group (subject 1), the time course is depicted in Fig. 2E. In the *WL-* group, the alpha ERSP at 10 Hz was highest in the last second of the retention interval. The time course with the alpha decrease in the first 2 s of the retention period is in line with a finding in a delayed choice task (Babiloni et al., 2005). Among electrodes AFz, Cz, Pz, and POz,

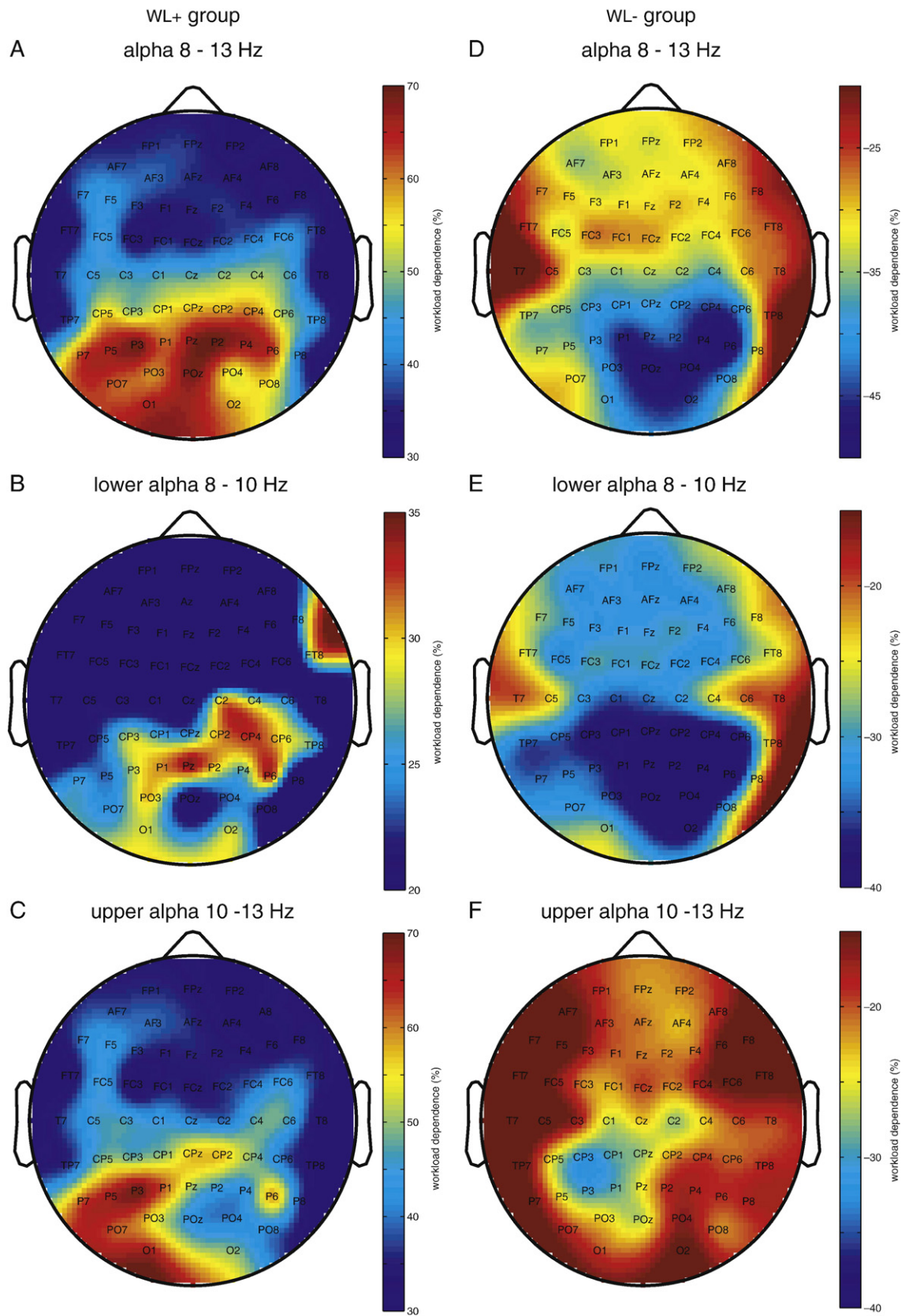


Fig. 5. Topography of workload dependence of alpha power. The parietal alpha maximum for the WL+ group (A–C) is strongest in the upper alpha band (C). The parietal alpha minimum for the WL– group (D–F) is strongest in the lower alpha band (E).



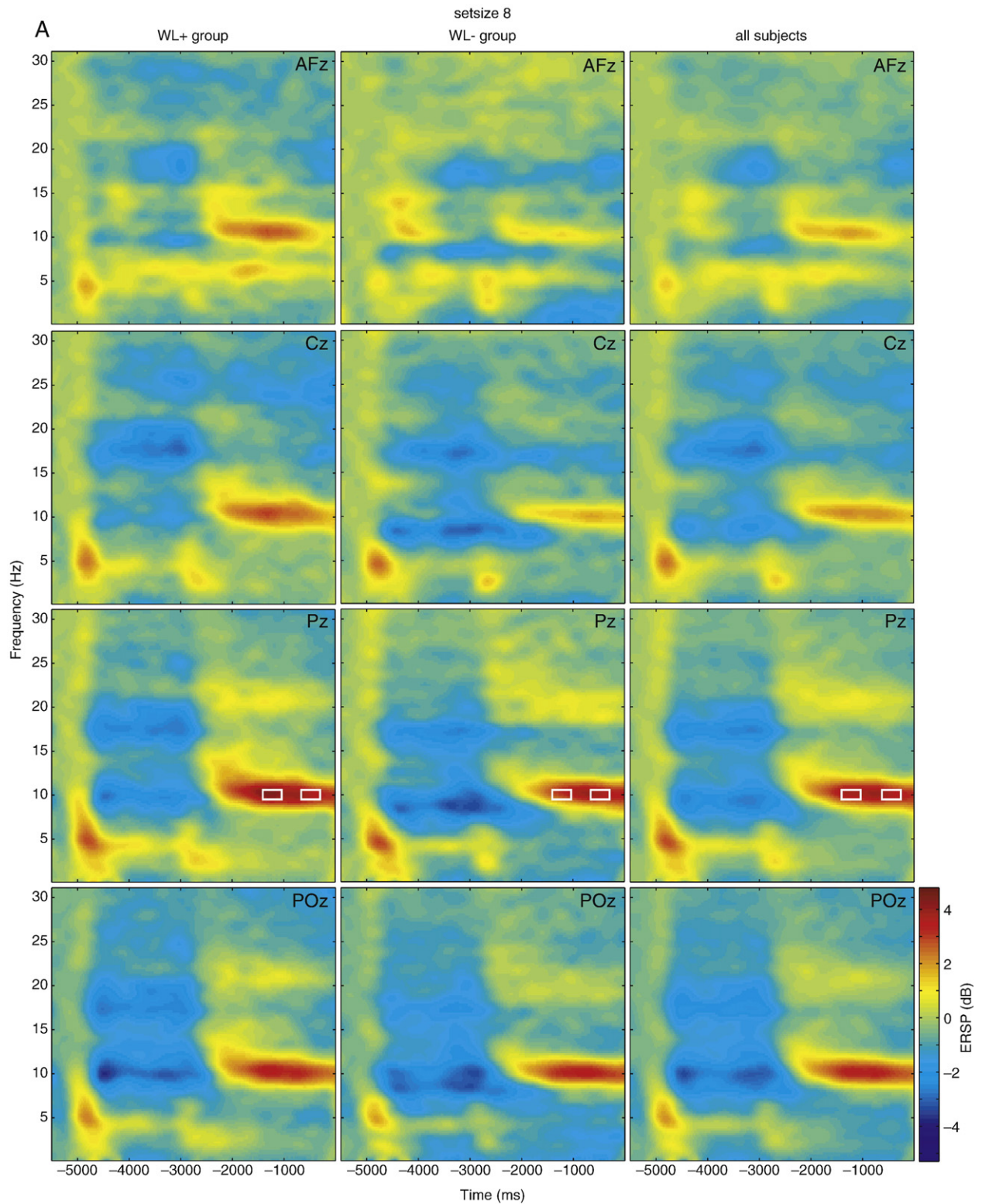


Fig. 6. Mean event-related spectral perturbation (ERSP) at electrodes AFz, Cz, Pz and POz for ss8 (A) and ss4 (B) with prestimulus fixation as baseline. At Pz for ss8, the alpha ERSP peak was early in the retention interval for the WL+ group and late for the WL- group. For the WL+ group, the ERSP decreases towards the end of the retention interval. For the WL- group, the ERSP increases towards the end of the retention interval. Rectangles indicate the time–frequency regions used to calculate the slope  $dP\alpha/dt$  of the ERSP in Table 1 ( $10 \pm 0.5$  Hz at  $1.3 \pm 0.2$  s and  $0.5 \pm 0.2$  s).

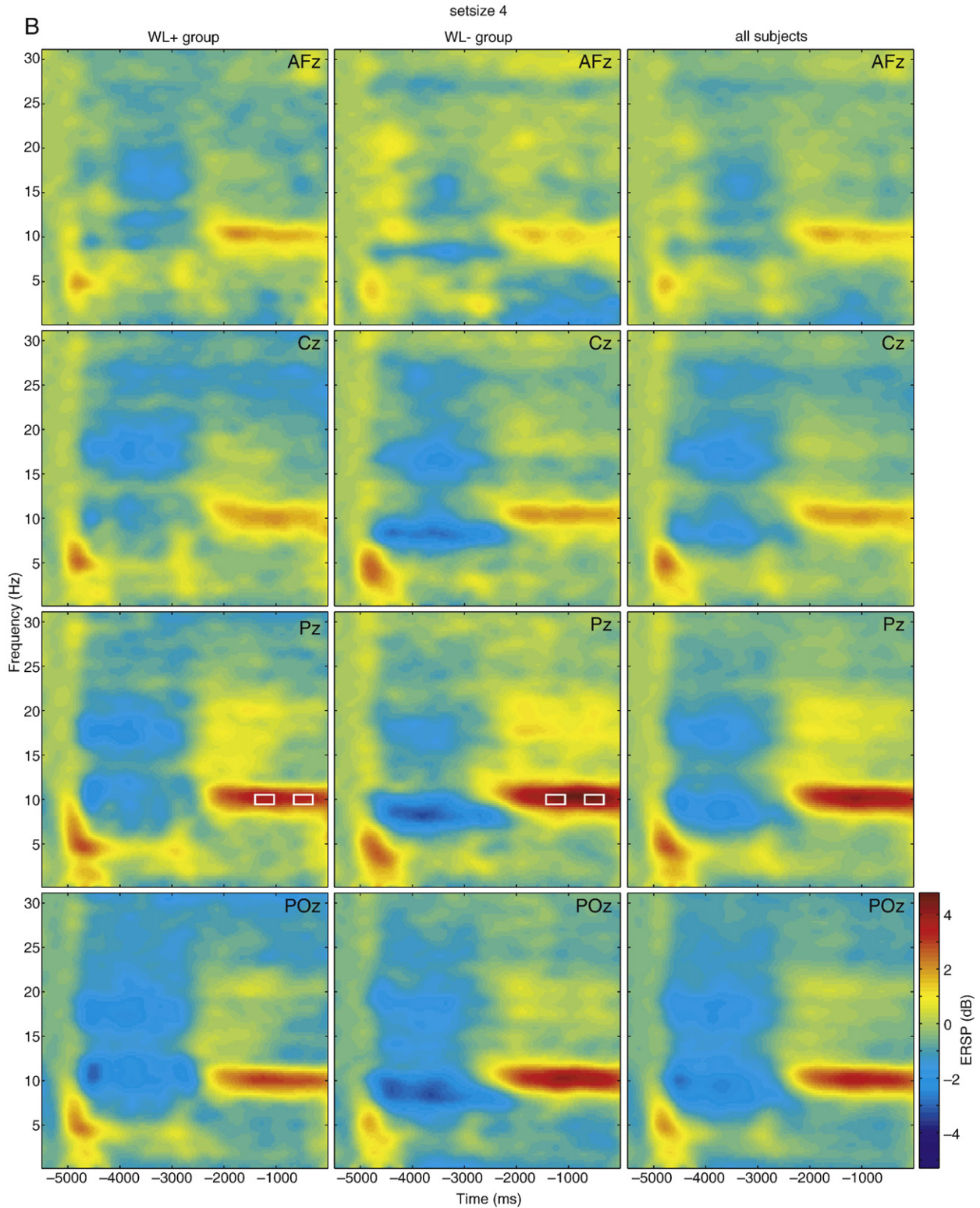


Fig. 6 (continued).

the time–frequency representation of the whole trial showed the strongest alpha ERSP at electrode Pz. Fig. 7 shows the time course of alpha activity for the two groups with the ERSP at electrode Pz calculated by the multitaper technique focused on the last 2 s of the retention interval.

To quantify the time course of the ERSP at Pz, we calculated the slope  $dP\alpha/dt$  of the alpha power  $P\alpha$  for ss8 trials of each subject (Table 1). Of the WL+ group, 7/9 subjects showed a negative slope and 7/9 subjects of the WL- group showed a positive slope. The difference between the groups is significant with  $p < 0.024$  (Wilcoxon

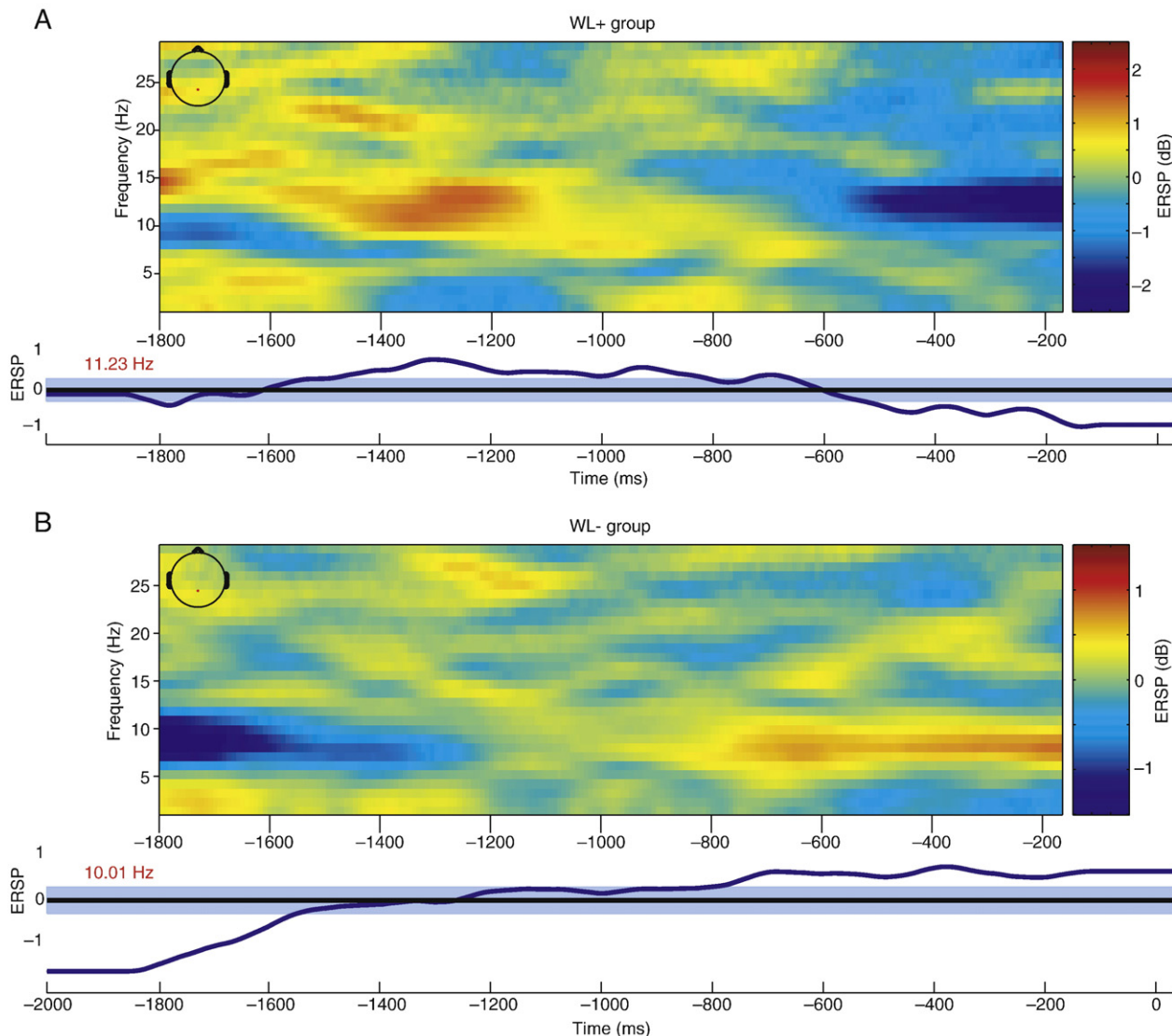


Fig. 7. Mean event-related spectral perturbation (ERSP) at electrode Pz for ss8 of the last 2 s of the retention interval. We used trial mean log power as baseline. Each single trial EEG time series was transformed to a spectrographic image using the multitaper method applied to short sliding time windows. We used a fixed window length of 400 ms, time resolution  $N=0.4$ , frequency resolution  $W=3$  and  $k=1$  taper. (A) For the WL+ group, the ERSP decreases towards the end of the retention interval. (B) For the WL- group, the ERSP increases towards the end of the retention interval. For both groups at their respective maximum frequencies, the effect exceeds the 95% confidence interval (blue ribbon in lower panels).

test). Also for ss4, 7/9 subjects of the WL- group showed a positive slope, pointing to the importance of ss4 trials for the workload dependence of alpha power in this group.

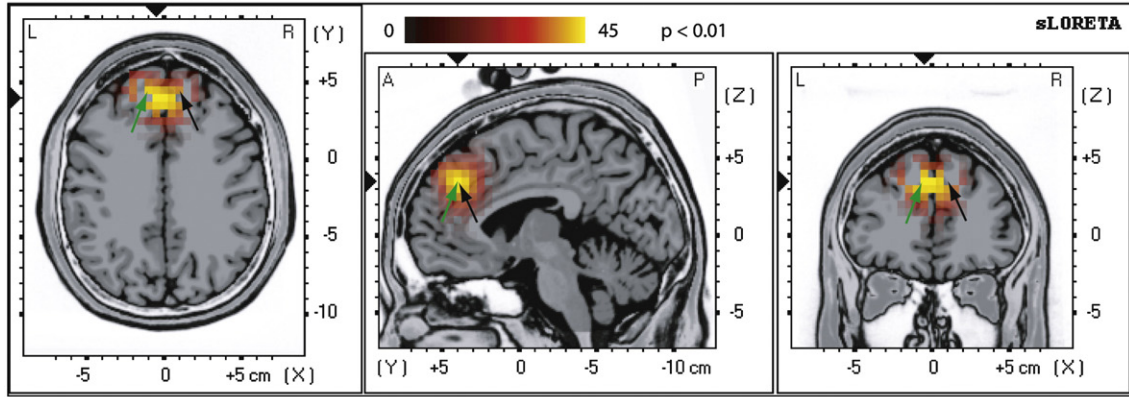
#### Cortical alpha generators

To identify the cortical generators of the alpha activity, we transformed the EEG of all subjects to sLORETA activations and calculated the contrast ss8 vs. ss4. We did this separately for the

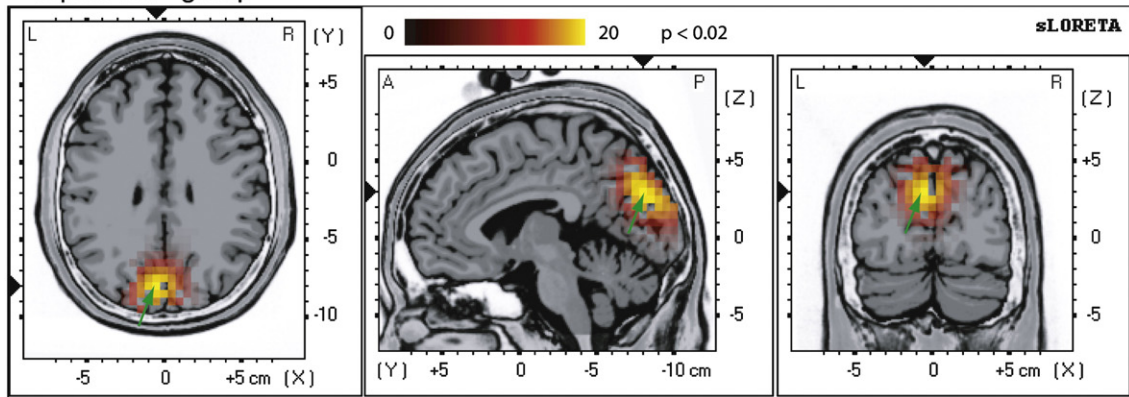
WL+ group (Fig. 8B) and for the WL- group (Fig. 8C). Taking into account the time course of the activations, we selected the interval from -2000 to -1000 ms for the WL+ group and the interval from -1000 to 0 ms for the WL- group. This selection had little influence ( $<1$  cm difference in all dimensions) on peak MNI coordinates as compared to analysis of the whole last 2 s of the retention interval. For the WL+ group, the activation showed a spectral peak at 10.5 Hz and a topographical maximum in the

Fig. 8. Paired group tests of sLORETA source analysis maps for ss8 compared to ss4 at the spectral peak. At cortical voxels  $t$ -values are color coded, the threshold was set at the  $p$ -value given at the color bar. (A) For the  $\theta$ IC, the maximal difference across the 18 subjects appeared in the dorsal part of the medial frontal gyrus (BA 9, MNI coordinates:  $x=-5, y=40, z=35$ ) at 6 Hz. When the subgroups were analyzed separately, the activation remained in the medial frontal gyrus for this contrast (WL+ group:  $p<0.01$ , peak activation at green arrow. WL- group:  $p=0.06$ , peak activation at black arrow). (B) For the WL+ group, activation difference was highest in the cuneus (BA 18/19, MNI coordinates:  $x=-5, y=-80, z=30$ , green arrow). (C) For eight subjects of the WL- group, the activation difference was highest in the precuneus (BA 7,  $x=5, y=-50, z=55$ , black arrows). The blue color bar indicates a decreased activation since trials with ss8 showed less alpha power than trials with ss4. (D) Average activity during the eyes-closed condition. The color bar shows sLORETA activation. For both groups the site of maximal activation (WL- group green arrow,  $x=5, y=-75, z=15$ ; WL+ group, black arrow,  $x=5, y=-80, z=20$ ) was located in the cuneus.

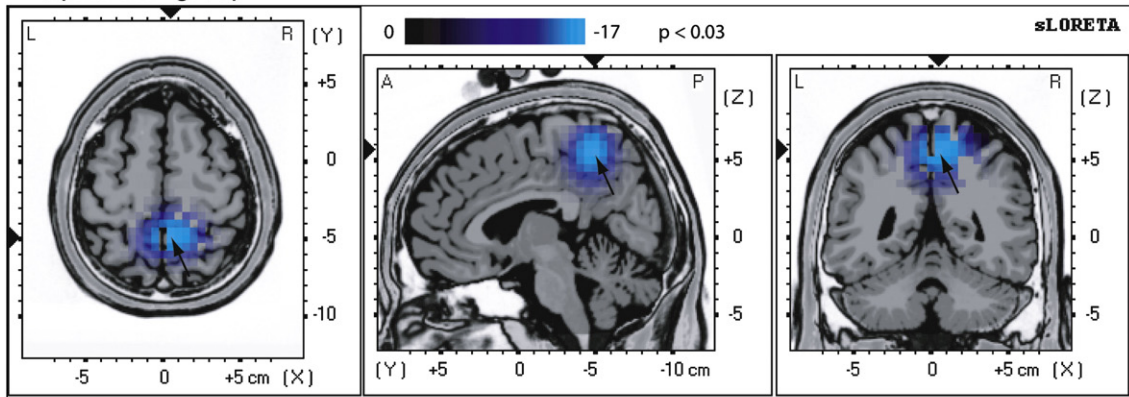
A theta all subjects



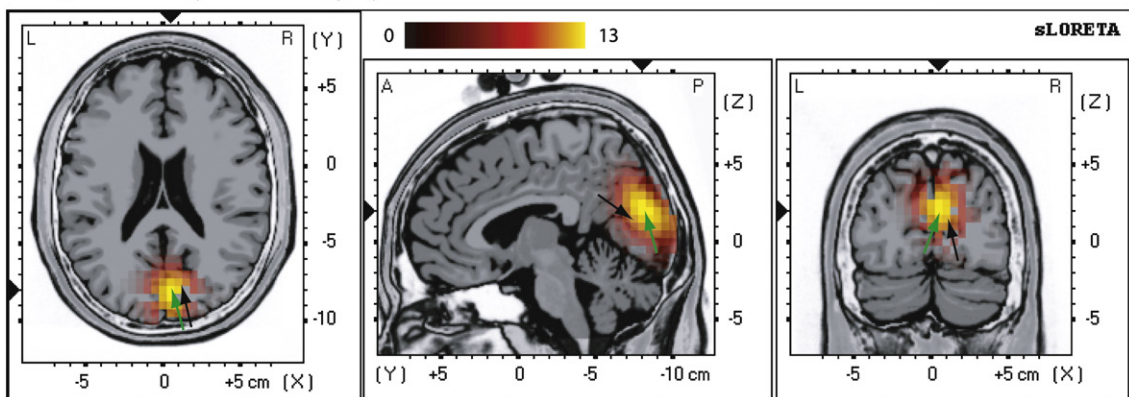
B alpha WL+ group



C alpha WL- group



D alpha all subjects resting eyes closed



cuneus (BA 18/19,  $p < 0.02$ ). For the WL− group the activation was maximal at 8.5 Hz in the precuneus (BA 7,  $p < 0.03$ ). For this analysis only 8 members of the WL− group were included since single-subject results revealed that subject 17 was an outlier with respect to activation for ss4. On an individual basis, the sLORETA maximum of 6/9 subjects of the WL+ group was located in BA 18/19, and in BA 7 for 6/9 subjects of the WL− group (Table 1).

#### Unrelated factors

We then asked whether the division in WL+ group and WL− group was due to factors unrelated to the WM task. First, there was no significant difference in performance between the two groups ( $p = 0.88$ , *t*-test). Second, we found no significant effect of gender ( $p = 0.35$ , *t*-test) or age ( $p = 0.34$ , *t*-test). Third, we controlled whether differences in the alpha peak between the WL+ group and the WL− group could be due to a difference in general alpha power level for the individual subjects. We found no difference in the average alpha power, neither for trials with ss4 ( $p = 0.68$ , *t*-test) nor for trials with ss8 ( $p = 0.59$ , *t*-test). Then we compared the resting EEG alpha peak at electrode Pz while subjects were relaxing with their eyes closed for 5 min. We found that (1) the absolute alpha peak height did not differ significantly between the two subgroups ( $p = 0.86$ , *t*-test) and (2) that there was no systematic shift in the alpha peak frequency between the two subgroups (mean peak frequency for the WL+ group:  $9.6 \pm 1.6$  Hz, WL− group:  $9.7 \pm 1$  Hz). Finally, we determined the generators of the alpha activity while subjects had their eyes closed. The average generator was located in the cuneus for both the WL+ and the WL− group (Fig. 8D). Whereas the peak location for the WL− group during the eyes closed condition strongly differed from that found during the WM task (peak MNI coordinates during eyes closed:  $x = 5$ ,  $y = -75$ ,  $z = 15$ , peak MNI coordinates during WM task:  $x = 5$ ,  $y = -50$ ,  $z = -55$ ), the peak location for the WL+ group was closer for these two conditions but was still distinct (peak MNI coordinates during eyes closed:  $x = 5$ ,  $y = -80$ ,  $z = 20$ , peak MNI coordinates during WM task:  $x = -5$ ,  $y = -80$ ,  $z = 30$ ). These results suggest that resting alpha activity is unrelated to the alpha activity accompanying the WM task.

## Discussion

#### *Theta increases with WM workload*

The increase in frontal theta power with memory load in this modified Sternberg task (Fig. 3) is in agreement with earlier EEG findings obtained for a large variety of WM tasks (Gevins et al., 1997; Klimesch, 1999; Krause et al., 2000; Kahana et al., 2001; McEvoy et al., 2001; Raghavachari et al., 2001; Fingelkurts et al., 2002; Jensen et al., 2002; Onton et al., 2005). The theta activity in the retention interval could be associated with one salient component by ICA. This association is evidence that one aspect of WM activity can be described by a distinct physiological process in a specific frequency band with a specific generator in the frontal cortex (Fig. 8A).

#### *Alpha increase may reflect WM maintenance or inhibition of task-irrelevant regions*

For the subjects of the WL+ group, the increase of alpha activity during WM retention (Table 1) is similar to what other authors have described (Jensen et al., 2002; Jokisch and Jensen, 2007; Tuladhar et al., 2007). Over time, we found that the maximum alpha power occurred in the middle of the retention interval and diminished towards the end of this period (Fig. 6A). This

time–frequency spectrum is similar to other WM studies using a modified Sternberg task (Klimesch et al., 1999; Jensen et al., 2002; Schack and Klimesch, 2002; Tuladhar et al., 2007).

What could be the role of alpha increase during WM retention? A first hypothesis is that increased alpha reflects WM maintenance. The argumentation that alpha emerges under conditions not involving memory does not exclude the possibility that alpha increase may reflect WM maintenance. In this study, alpha activation was centered in an occipital area, namely BA 18/19, which is an area involved in the processing of complex visual features as well in other cognitive processes. Additionally, the activation extends to the ventral part of the precuneus (BA 7), thus was not only limited to visual areas. Also in the study of Jensen et al. (2002), workload-dependent increases were found over parietal sensors as well as in occipital sensors. In two recent fMRI studies bilateral activation was found in the cuneus during WM tasks (Tomasi et al., 2006; Lagopoulos et al., 2007). In one study, stronger cuneus activation was reported for high-workload conditions (Tomasi et al., 2006).

A second hypothesis is that the workload-dependent increase of alpha reflects functional inhibition. The alpha peak frequencies (mean 10.4 Hz, Table 1) are in the range termed upper alpha band, where correlates of inhibition have been reported (Klimesch et al., 1999; Jensen et al., 2002; Klimesch et al., 2005). It has been proposed that once capacity limits of WM are reached, potentially interfering, task-irrelevant brain areas are inhibited and that alpha oscillations represent an active filter mechanism (Klimesch et al., 2007). This hypothesis is supported by the finding that alpha power may increase contralaterally to the hemifield where a visual stimulus has to be ignored (Worden et al., 2000; Kelly et al., 2006; Thut et al., 2006; Rihs et al., 2007) and also two MEG studies which suggest that alpha activity can reflect suppression of processing in visual areas (Jensen et al., 2002; Tuladhar et al., 2007).

The generator of the alpha activity in the subjects of the WL+ group was located in the cuneus (Fig. 8B). We assume that the visual areas located in the cuneus are less relevant for this WM task, which engages mainly the phonological loop (Baddeley, 2003). Thus, alpha increase would reflect active inhibition of the cuneus as a task-irrelevant region. Conversely, we may take the amount of variance explained by the  $\theta$ IC as a marker for a cognitive resource related to WM maintenance in a task-relevant region, i.e. prefrontal cortex. Indeed, the amount of variance explained by the  $\theta$ IC was significantly higher in the WL+ group than in the WL− group (Table 1). We thus propose that, for the subjects of the WL+ group, disengagement of the cuneus liberates cognitive resources in prefrontal cortex needed for correct performance in the WM task.

#### *Workload-dependent alpha decrease reflects attention*

Retaining a string of 8 letters in memory also requires more attention than retaining a string of 4 letters. Alpha decrease has been observed in response to a variety of non-task and non-stimulus-specific factors, which may be best subsumed under the term attention (Klimesch, 1999; Klimesch et al., 2007). Furthermore, our finding of the workload-dependent alpha decrease around 8.9 Hz in the WL− group is in line with the description of lower alpha as related to attentional factors (Klimesch, 1999). Also other WM tasks may lead to a decrease in alpha (Gevins et al., 1997; McEvoy et al., 2001; Bastiaansen et al., 2002) and may also

have been related to increased attentional demand. For example in the study of Gevins et al., subjects performed a continuous memory task (*n*-back task) which requires more continuous attention than the Sternberg task (Gevins et al., 1997).

The cortical generator of alpha activity was located in the precuneus in the WL− group (Fig. 8C). This is compatible with the evidence that the precuneus is involved in several tasks requiring enhanced attention (Chee and Chuah, 2007). Furthermore, reduced alpha has been shown to correlate with increased BOLD activity in the precuneus for a task very similar to ours (Meltzer et al., 2007). This supports the view that lower alpha band activity in the WL− group reflects release of functional inhibition (Klimesch et al., 2007). We may then speculate that the alpha decrease found in this group during the retention interval would release the precuneus as a task-relevant area from inhibition. In this disinhibited state the precuneus should then be able to better provide its functional contribution to the attentional network required for WM task performance.

#### *Gradual transition between alpha processes or two distinct alpha processes?*

We have stratified our subjects into two groups based on the workload dependence of alpha power. The stratification gains meaning by the fact that the observables 1) theta variance explained by  $\theta$ IC, 2) alpha peak frequency, and 3) ERSF slope  $dPa/dt$  in Table 1 show significant differences between the two groups. The three observables are in their measurement unrelated to the workload dependence of alpha power. The statistically significant difference leads us to reject the hypothesis that the values stem from identical continuous distributions with equal medians. This speaks for two distinct processes involved in the two groups of subjects. The distinction between the two processes is lost if all subjects are grouped in a grand average (Fig. 4). The low regression coefficients in Table 1 for most observables do not support a gradual transition between brain processes in different subjects. The localization of cortical alpha generators supports the stratification not in all but in the majority of subjects. We have, however, no reason to exclude that all subjects use both processes. We therefore propose that subjects of the two groups draw on the two types of alpha processes to different extent.

#### **Conclusions**

In this study, we report evidence that both theta activity and alpha activity are modulated by WM load. In particular, we found support for two distinct patterns of alpha activity in different subjects. We suggest that in the subjects of the WL+ group, increased alpha activity reflects active functional inhibition in a task-irrelevant region (cuneus). Conversely, in the subjects of the WL− group, workload-dependent decrease of alpha activity might reflect disinhibition of a task-relevant area (precuneus), which can then fulfill increased attentional demands. In their effort to solve the task, subjects of the two groups seem to have expressed these two types of alpha processes to different extent. Since averaging renders the two different processes invisible, care should be taken when grouping individual subject data into the grand average. New tasks and methods of analysis will have to be devised to characterize these brain processes in different subjects. While the comparison between results of different studies in the literature is complicated by the different tasks used, our study reveals two types of alpha activity for the same task.

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