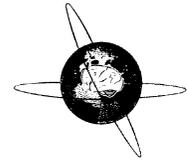




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Human cortical responses during one-bit short-term memory. A high-resolution EEG study on delayed choice reaction time tasks

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Abstract

Objective: We investigated whether a very simple short-term memory (STM) demand induces a visible change of EEG rhythms over the two hemispheres.

Methods: High-resolution EEG was obtained in young adults during two delayed choice reaction time tasks. In the STM condition, a simple cue stimulus (one bit) was memorized along a brief delay period (3.5–5.5 s). The task was visuo-spatial in nature.

Results: In the control (NSTM) condition, the cue stimulus remained available along the delay period. Compared to the control condition, the theta power (4–6 Hz) decreased in left frontal and bilateral parietal areas (delay period). Furthermore, low alpha power (6–8 Hz) decreased in bilateral frontal and left parietal areas, while high alpha power (10–12 Hz) decreased in the left fronto-parietal areas.

Conclusions: The decrease of the alpha power is as an expression of the efficient information transfer within thalamo-cortical pathways. The significance of the study stands in the fact that even a very simple STM task (only one bit to be memorized) revealed changes in fronto-parietal theta and alpha rhythms.

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Keywords: Short term memory; Delayed choice reaction time; Cerebral cortex; Electroencephalography; Theta rhythm; Alpha rhythm; Event related desynchronization/synchronization

1. Introduction

Short-term memory (STM) can be easily investigated by the so-called delayed reaction time task (Goldman-Rakic, 1987, 1991). The subject has to retain a cue stimulus and a related motor response across a delay period up to an imperative go stimulus. In the STM variant of the task, the cue stimulus rapidly disappears. In the control variant, the cue stimulus is delivered along the whole delay period. With respect to ‘delayed match-to-sample’ and ‘n-back’ STM paradigms, the delayed reaction time tasks include

no on-line probe stimulus to be matched with the memorized cue stimulus. The delayed reaction time tasks have been successfully used for the study of cognitive processes in schizophrenia and aging (Goldman-Rakic, 1991; Servan-Schreiber et al., 1996; Roux et al., 1994; Harrington et al., 2000).

Neurobiological correlates of the delayed reaction time tasks have been extensively investigated in non-human primates (Mishkin, 1957; Funahashi et al., 1989, 1990, 1993). It was shown that prefrontal and posterior parietal areas play a key role in the maintenance of the ‘representational memory’ during the delay period (Mishkin, 1957; Butters and Pandya, 1969; Goldman-Rakic, 1988; Fuster, 1995; Funahashi et al., 1989, 1990, 1993; Kessels et al.,

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2000). Furthermore, lesional studies in rats have shown that the delayed reaction time tasks rely on loops encompassing cortex, thalamus, and basal ganglia (Mair et al., 1998; Burk and Mair, 1999).

Thalamo-cortical activity during delayed reaction time tasks has been explored by recent electroencephalographic (EEG) studies in humans (Filipovic et al., 2001; Bastiaansen et al., 2002). An experiment included a sequence of Go or Nogo stimuli, delay period, and imperative stimulus triggering motor (Go trials) or no (Nogo trials) responses. During the delay period of both conditions, fronto-parietal alpha power (8–12 Hz) gradually decreased as a reflection of the desynchronizing drive of the thalamus on cortex (Filipovic et al., 2001). In another experiment, subjects had to remember the spatial feature of a cue stimulus along the delay period (Bastiaansen et al., 2002). Theta (4–6 Hz) and alpha (6–8 Hz) power decreased in fronto-parietal areas, more during the STM than control condition. These results were surprising since the theta power usually increases during mental effort and high memory workload, mainly as an effect of a fronto-hippocampal drive (Pfurtscheller and Klimesch, 1992; Gevins et al., 1997; Gevins and Smith, 2000; McEvoy et al., 2001).

In this high-resolution EEG study, young adults were given a very simple STM variant of the delayed reaction time task. The memory task was essentially visuospatial in nature, although a parallel minor phonological and sensorimotor coding of the memory traces could not be excluded. This task included a sequence of cue stimulus (two vertical bars), delay period ('blank screen' for few seconds), go stimulus, and motor response compatible with the taller vertical bar. Only one bit of information had to be retained. In the control (NSTM) task, the cue stimulus remained on the screen along the delay period up to the go stimulus. The present experiment tests the hypothesis that a very simple STM demand could induce a visible change of the fronto-parietal theta and alpha oscillations in young normal subjects.

2. Materials and methods

2.1. Subjects

Experiments were performed in 14 healthy, right-handed (Edinburgh Inventory) adults, who gave their informed written consent according to the declaration of Helsinki. The mean age was 30.1 years (± 1.4 standard error, SE), the mean education level was 12.6 years (± 1.1 SE) and the mean handedness score was 92.5% (± 0.9 SE). The number of subjects was reduced to 12 (see below). The local institutional ethics committee approved general procedures.

2.2. Experimental tasks

Subjects were seated in a comfortable reclining armchair, placed in a dimly-lit, sound-damped, and

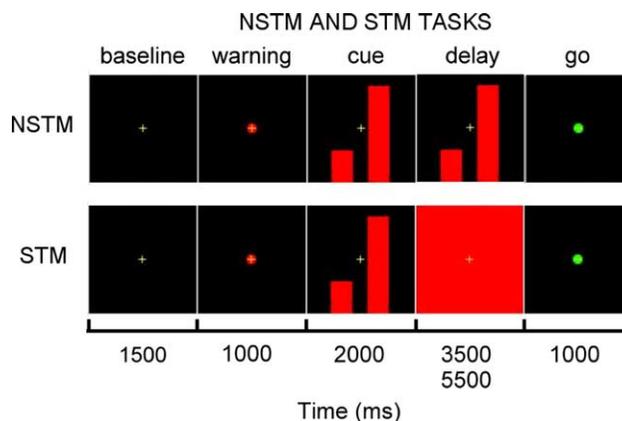


Fig. 1. Setup and experimental tasks. The experiment included a short-term memory (STM) task compared to a control (NSTM) task. The sequence of events for the STM condition was as follows: (i) a cross at the center of the monitor as a visual warning stimulus lasting 1 s, (ii) a couple of vertical bars as a visual cue stimulus lasting 2 s, (iii) a blank screen as a delay period lasting 3.5–5.5 s, (iv) a circle at the center of the monitor as a go stimulus lasting 1 s, and (v) a finger movement as a motor response. Subjects had to click either left mouse button if the taller bar was at the left monitor side or right mouse button if the taller bar was at the right monitor side. Compared to the STM task, the NSTM task had visual cue stimuli lasting up to the go stimulus.

electrically-shielded room. They kept their forearms resting on armchairs, with right index finger resting between two buttons spaced 6 cm each other. A computer monitor was placed in front of them (about 100 cm). The STM task (Fig. 1) comprised a sequence of baseline stimulus (a 0.7° cross at the center of the monitor), visual warning stimulus (the cross was surrounded by a circle for 1 s), visual cue stimulus (two vertical bars large about 2° and height $2.5\text{--}7^\circ$ for 2 s), delay period (blank screen for 3.5–5.5 s), go stimulus (the circle appeared again for 1 s), and right finger movement to press the proper button. Subjects had to click left mouse button if the taller bar (cue stimulus) was at the left monitor side, whereas they had to click the right mouse button if the taller bar was at the right monitor side. In the NSTM condition, the visual cue stimulus was delivered up to the go stimulus. Two trial blocks for each condition were pseudo-randomly intermingled (block = 50 single trials; 2 min pause). Subjects were told in advance if the block was NSTM or STM. The global luminance of the monitor was kept practically uniform across the two conditions (i.e. the changes of the scene were limited to the form) and was measured direct on the monitor by a Tektronic J17 and J1800 Series LumaColor Photometer.

Before the recording session, a training period of about 10 min familiarized the subjects with the experimental apparatus and tasks.

2.3. EEG recordings

EEG data were recorded (0.1–60 Hz bandpass; 256 Hz sampling frequency) with a 46-tin-electrode cap referenced

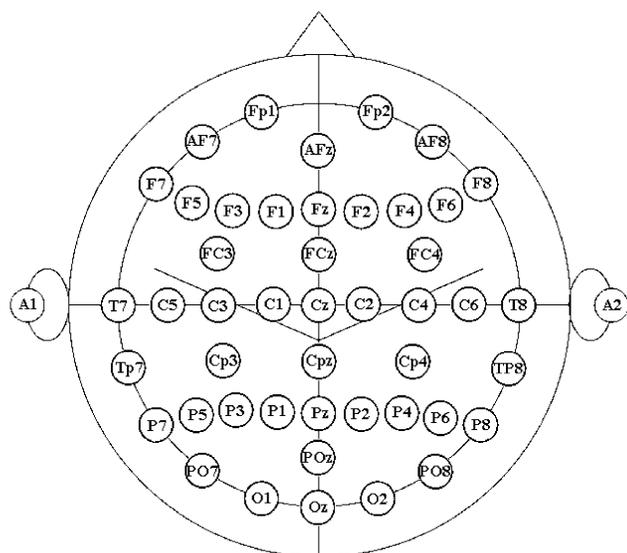


Fig. 2. Diagram showing the 46 electrodes (augmented 10–20 System) used for the present experiments. The position of the labels in the list roughly represents the position of the corresponding electrodes over the scalp. Of note, a hyphen between two electrode labels indicates that the electrode is located halfway between the two labeled electrodes.

to linked ears. The electrodes were positioned according to an augmented 10–20 system (Fig. 2) and electrode impedance was kept lower than 5 k Ω . The positions of the electrodes and landmarks were digitized.

Electrooculogram (0.1–60 Hz bandpass; 256 Hz sampling frequency) and surface electromyographic activity of bilateral extensor digitorum muscles (1–60 Hz bandpass; 256 Hz sampling frequency) data were also collected. The electrooculogram (EOG) monitored blinking or eye movements, whereas the electromyogram (EMG) monitored the voluntary movements as well as involuntary mirror movements and muscle activations.

2.4. Off-line preliminary data analysis

The EEG epochs were automatically and manually rejected. The computerized automatic procedure was based by a software package that included automatic procedures for (i) EOG artifact detection and correction, (ii) EMG analysis, (iii) EEG artifact analysis, (iv) optimization of the ratio between artifact-free EEG channels and trials to be rejected. The reject criteria were based on a threshold method and on a statistical method evaluating the non-stationarity of the EEG signal (Moretti et al., 2003). Then, two expert electroencephalographers manually confirmed the automatic selections (inter-rater reliability higher than 95%). The EEG epochs contaminated by these artifacts were removed. Spatial resolution of artifact-free EEG data was enhanced by surface Laplacian estimation (regularized 3-dimensional spline function; Babiloni et al., 1996, 1998). The surface Laplacian estimation acts as a spatial filter that reduces head volume

conductor effects and annuls electrode reference influence (Nunez, 1995; Babiloni et al., 1996, 1999, 2000, 2001a, 2001b, 2002). In some cases, the Laplacian values at the border electrodes were zeroed due to the unreliability of the spline Laplacian estimate at these electrodes.

The single trial analysis was carefully repeated on the Laplacian-transformed EEG data, to discard the single trials contaminated by residual computational artifacts. In 2 out of 14 subjects, the number of artifact-free EEG single trials was insufficient (i.e. lower than 30% of the individual data set). Consequently, the EEG data of 12 subjects were further considered for the final data analysis. The mean of the artifact-free EEG data was of 82 (± 12 SE) single trials for the STM task and of 68 (± 10 SE) single trials for the NSTM task (no statistical difference; $F(1, 11) = 2.75$; $P = 0.15$). Motor reaction time after the go stimulus was computed for all artifact-free EEG single trials.

2.5. Determination of individual alpha bands

Frequency bands of interest were theta, alpha 1, alpha 2, and alpha 3, whose band limits were computed according to a standard procedure based on the peak of individual alpha frequency (IAF; Klimesch, 1996, 1999; Klimesch et al., 1998). The IAF was defined as the frequency showing maximum power density peak within extended alpha range (6–14 Hz). The across subject mean values of IAF, which was computed across baseline, warning, cue, and delay periods, were of 10.6 (± 0.3 SE) for both STM and NSTM conditions. With respect to the IAF, the frequencies of interest were (i) theta as IAF – 6 Hz to IAF – 4 Hz (4.6–6.6 Hz), (ii) alpha 1 as the IAF – 4 Hz to IAF – 2 Hz (6.6–8.6 Hz), (iii) alpha 2 as IAF – 2 Hz to IAF (8.6–10.6 Hz), and (iv) alpha 3 as IAF to IAF + 2 Hz (10.6–12.6 Hz). The power spectrum analysis was based on a FFT approach using Welch technique and Hanning windowing function.

2.6. Computation of event-related desynchronization/synchronization (ERD/ERS)

To quantify the event-related changes of EEG power, a popular procedure was used, namely the computation of event-related desynchronization/synchronization (ERD/ERS; Pfurtscheller and Aranibar, 1979; Pfurtscheller and Neuper, 1994; Pfurtscheller et al., 1997). The ERD/ERS of the individual theta, alpha 1, alpha 2 and alpha 3 bands was computed as follows: Laplacian EEG time series were bandpassed (Bartlett function), squared, averaged across 120 ms periods (8 samples/s), and averaged across all single trials. The ERD/ERS was defined as the percentage decrease/increase of instant power density at the ‘event’ compared to a ‘pre-event’ baseline (from –2 to –1 s).

A spline interpolating function (Babiloni et al., 1995) determined individual ERD/ERS values at theoretical 46 sites of augmented 10–20 system. This procedure has some important advantages and a minor disadvantage.

It provided ERD/ERS values exactly at the same scalp sites across the experimental subjects, thus overcoming the spatial errors due to the individual shift of the positioning of the electrode cap. Furthermore, these sites could be aligned with respect to a cortical map coded into Talairach space. In that Talairach space, the electrode sites F3, F4, P3, and P4 overlaid dorsolateral prefrontal and posterior parietal areas. As a disadvantage, spline functions might introduce some minor estimation errors. However, these errors may be negligible here, given the relative small distance between real and theoretical electrode positions and the fact that these possible errors were paired in the experimental and control conditions. These electrodes were displaced over a 3-dimensional head model approximating each 'realistic' individual head model. This template model was constructed based on the magnetic resonance data of 152 subjects, digitized at Brain Imaging Center of the Montreal Neurological Institute (SPM96).

2.7. Measurement of ERD/ERS amplitude

The theta and alpha ERD/ERS waveforms were analyzed to disclose the typical sequence of ERD peak (T1) followed by a reduced ERD or a true ERS peak (T2). In the present case, this sequence was expected as maximum during the delay period of the STM condition. The ERD peak was defined as the maximum ERD value during the delay period. While, the ERS peak was defined as the minimum ERD value or maximum ERS value (if any) during that period. For sake of brevity, we called ERS peaks both reduced ERD and true ERS.

The ERD and ERS peaks (T1 and T2) were independently recognized by two experimenters (inter-rater reliability higher than 95%) within frontal and parietal regions of interest (ROIs). These ROIs included (i) F5, F3 and F1 electrodes for the left frontal region or FL, (ii) F6, F4 and F2 electrodes for the right frontal region or FR, (iii) P5, P3 and P1 electrodes for the left parietal region or PL, and (iv) P6, P4 and P2 electrodes for the right parietal region or PR. The ERD/ERS amplitude was automatically measured for each experimental condition at each of the 46 electrodes. The ROI having the maximal ERD/ERS values was considered as a reference for the latency of the topographical mapping. This latency was the instant of the delay period showing the maximum alpha ERD amplitude.

2.8. Statistical analysis

Statistical comparisons were performed by analysis of variance (ANOVA) for repeated measures. Mauchley's test evaluated the sphericity assumption and the correction of the degrees of freedom was made by Greenhouse-Geisser procedure. Duncan test was used for post hoc comparisons ($P < 0.05$) only for the statistically significant interaction of the ANOVA analysis ($P < 0.05$).

Dependent variables for the evaluation of the behavior were the percent of correct responses and the type of errors. For the errors, the ANOVA comprised factors Condition (NSTM, STM) and Error type (Wrong responses, No response, Delayed response). For the evaluation of movement reaction time only the factor Condition (NSTM, STM) was used.

The analysis of the ERD/ERS amplitude was performed by ANOVA analyses for theta, alpha 1, alpha 2, and alpha 3. The ERD/ERS amplitude of the responsive electrodes belonging to the same ROI was averaged. The number of the responsive electrodes was the same for all the ROI. The ANOVA factors were Condition (NSTM, STM), ROI (FL, FR, PL, PR), and Time (peaks).

3. Results

3.1. Behavioral results

There was no statistical difference in correct responses between conditions ($F(1, 11) = 0.58$; $P = 0.45$), namely 95% (± 2 SE) and 93% (± 4 SE) for the NSTM and STM tasks, respectively. Neither there were statistical differences in the error type ($F(1, 11) = 0.59$; $P = 0.47$).

The reaction time was shorter ($F(1, 11) = 11.402$; $MSe = 1026$; $P < 0.007$) during the NSTM (604 ms ± 26 SE) than STM (650 ms ± 35 SE) condition. Therefore, this parameter was used as a covariate for the statistical analysis of ERD/ERS amplitude.

3.2. Temporal evolution of visual evoked potentials

Fig. 3 shows the group waveforms of the visual evoked potentials (0.5–30 Hz bandpass) during the visual warning stimulus, cue stimulus, delay period, and go stimulus of the NSTM and STM tasks. Representative parietal and occipital electrodes were considered. The VEOG and HEOG are also plotted, in order to emphasize the absence of ocular movements.

Notably, the amplitude of the visual evoked potentials returned at baseline values before the end of the cue period. Therefore, these phase-locked potentials could not affect the ERD/ERS during the delay period. Of note, the offset of the present cue stimulus did not evoke any potential.

3.3. Temporal evolution of ERD/ERS

Figs. 4 and 5 show the group ERD/ERS waveforms of the theta, alpha 1, alpha 2, and alpha 3 for the NSTM and STM conditions. These waveforms refer to representative frontal and parietal electrodes. Substantial alpha and theta ERS values were observed during the warning and cue periods, affected by the visual evoked potentials. Moreover, the transient alpha ERD/ERS across warning and cue periods (i.e. mainly evoked by phase-locked EEG potentials) could

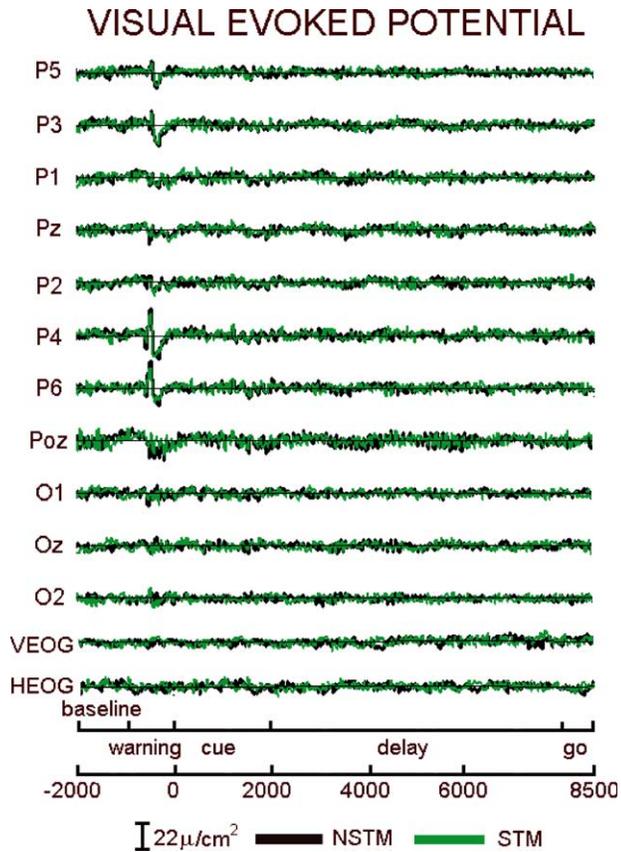


Fig. 3. The grand average waveforms of Laplacian visual evoked potentials (0.5–30 Hz bandpass) for the NSTM and the STM conditions. These waveforms refer to representative parietal and occipital electrode sites. The grand average waveforms of VEOG and HEOG are also reported.

differ between the two conditions due to different levels of attention or visual demand implicated by the STM respect to NSTM tasks. Indeed, the subjects knew in advance if the recording block was STM or NSTM. According to the scope

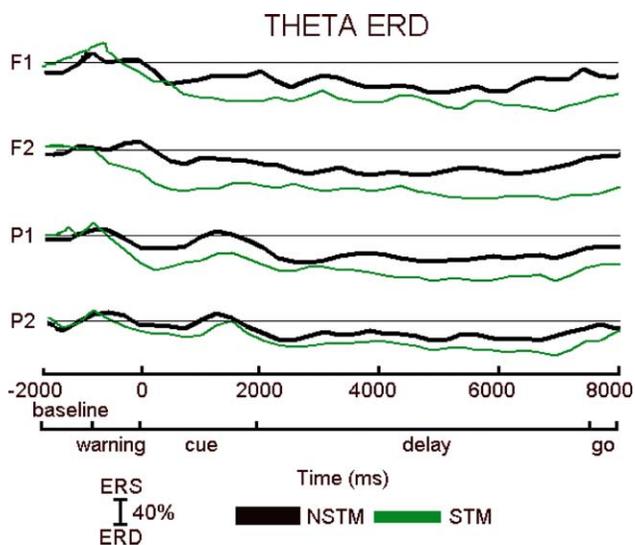


Fig. 4. The grand average waveforms of the theta event-related desynchronization (ERD) for the NSTM and STM conditions. These waveforms refer to representative frontal and parietal electrode sites.

of the present study, the focus of our analysis was on the delay period, which was relatively free from the mentioned transient alpha ERD/ERS. During the period of interest (delay period), the theta waveforms showed a long lasting ERD having maximal amplitude at parietal electrodes. Of note, one individual data set had no theta reactivity and was not further considered. On the other hand, the alpha ERD/ERS waveforms disclosed an ERD peak (T1) followed by a reduced ERD or a true ERS peak (T2). For the sake of brevity, we called ERS peaks both reduced ERD and true ERS. Both theta and alpha ERD values were maximal during the delay period of the STM.

3.4. Spatial distribution of ERD/ERS

Figs. 6 and 7 illustrate the topographical maps of the theta and alpha ERD/ERS peaks during the delay period. The theta ERD peak was widely distributed over the scalp, the amplitude being stronger over the parietal areas for the STM than NSTM condition. On the other hand, the alpha ERD peak (time 1, T1) was mainly represented over the left central and parietal areas. Afterward its peak, the ERD amplitude markedly reduced over the whole scalp up to the ERS peak (time 2, T2). The maps for the STM condition were principally characterized by a stronger alpha ERD peak (T1) in left parietal area and a less reduction of the alpha ERD at T2.

3.5. Statistical analysis of ERD/ERS during the delay period

Analysis of covariance (ANCOVA) pointed to a stronger theta ERD peak for the STM than NSTM condition during the delay period (main effect Condition, $F(1, 10) = 5.22$; $MSe = 788$; $P < 0.04$). Furthermore, there was just a statistical trend ($P < 0.07$) between the factors Condition (STM, NSTM) and ROI (FL, FR, PL, PR), which was not further considered.

During the delay period, the alpha 1 ERD/ERS peaks showed a statistically significant interaction ($F(3, 33) = 3.57$; $MSe = 79$; $P < 0.025$) among the factors Condition (NSTM, STM), ROI (FL, FR, PL, PR), and Time period (ERD peak or T1, ERS peak or T2). Fig. 8 (top) illustrates the means (\pm SE) of the ERD/ERS representing these results. For this statistically significant ANOVA interaction, Duncan post hoc testing indicated that the ERD peak (T1) was stronger for the STM than NSTM condition in right frontal ($P < 0.05$) and left parietal ($P < 0.005$) areas. The ERD values were also stronger for the STM than NSTM condition at ERS peak (T2), reaching a high statistical significance in left frontal ($P < 0.0005$), right frontal ($P < 0.005$), and left parietal ($P < 0.0005$) areas.

The alpha 2 ERD/ERS amplitude showed no statistical effect including the factor Condition ($P > 0.05$) during the delay period.

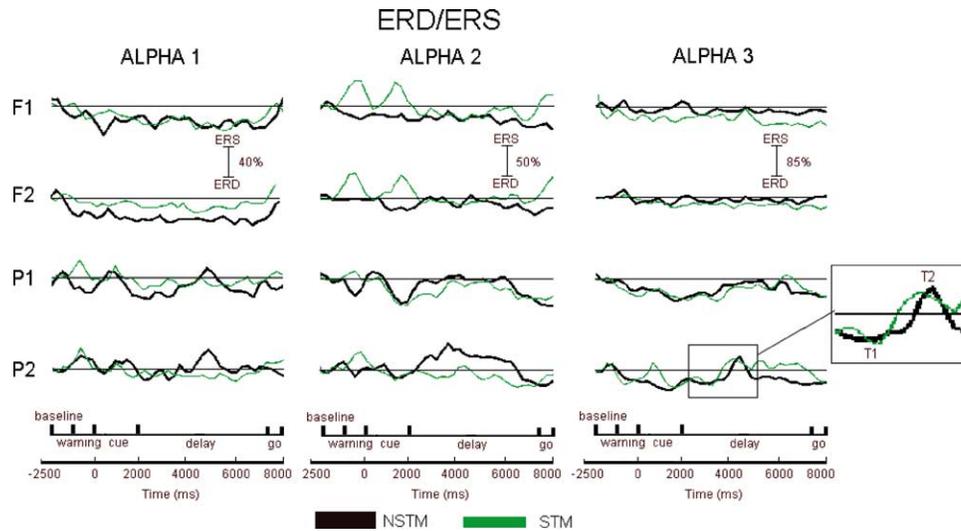


Fig. 5. The grand average waveforms of the alpha 1, alpha 2 and alpha 3 ERD/ERS (event-related synchronization, ERS) during the NSTM and STM conditions. These waveforms refer to representative frontal and parietal electrode sites. The inset shows an enlargement of the ERD peak followed by a ERS peak at a parietal electrode.

During the delay period, the alpha 3 ERD/ERS amplitude presented a statistically significant interaction ($F(3, 33) = 3.47$; $MSE = 176.8$; $P < 0.03$) among the factors Condition (NSTM, STM), ROI (FL, FR, PL, PR), and Time period (T1, T2). Fig. 8 (bottom) illustrates the means (\pm SE) of these ERD/ERS results. For this statistically significant ANOVA interaction, Duncan post hoc testing indicated that the ERD peak (T1) was stronger for the STM than NSTM condition in the left frontal ($P < 0.05$) and parietal ($P < 0.05$) areas. Along the delay period (T2), the ERD values continued to be stronger for the STM than NSTM condition in the left frontal area ($P < 0.05$), whereas true ERS values were stronger for the STM than NSTM condition in the right parietal area ($P < 0.0005$).

As a control, 3 ANCOVA analyses demonstrated that the above findings were not due to a different baseline band power of the theta, alpha 1, and alpha 3 oscillations.

4. Discussion

4.1. New evidence on theta ERD during delayed choice reaction time

Despite a so low memory load (one bit) during the STM delay period, there were differences in theta ERD respect to the NSTM condition. The STM condition induced a theta ERD stronger in the left frontal and bilateral parietal areas. These results confirm and extend those of a recent low-resolution EEG study using delayed response tasks with low memory load (Bastiaansen et al., 2002). Here the theta ERD prevailed in STM over NSTM condition not only in frontal but also in parietal areas, which could be probed with a more fine topographical detail than in the mentioned study

(Bastiaansen et al., 2002). On the other hand, the present results apparently contrast with the increase of the theta oscillations reported by other authors during transient memory load (Gevins et al., 1997; Klimesch, 1999; Gevins and Smith, 2000; Krause et al., 2000; McEvoy et al., 2001). This may be due to the difference among the present and previous experimental paradigms. Gevins' group has studied working memory in the framework of matching to sample or n-back paradigms having a marked retention load when compared to simple delayed response paradigm of the present study (Gevins et al., 1997; Gevins and Smith, 2000; McEvoy et al., 2001). Furthermore, Klimesch (1999) has found a theta increase during a long-term memory task of encoding-retrieval type. Finally, Krause et al. (2000) have found a theta increase during a short-term verbal memory task. On the whole, theta rhythm reactivity seems to be a promising feature to characterize the physiological mechanisms underlying various kinds of short-term memory paradigms in verbal and visuo-spatial domains.

Notably, the increase of the cortical theta is generally associated with the involvement of reciprocal cortico-(para)hippocampal loops during mental effort and memory (Green and Arduini, 1954; Petsche et al., 1962; Miller, 1991; Treves and Rolls, 1994; Bastiaansen and Hagoort, in press; Bastiaansen et al., 2002). Therefore, the present fronto-parietal theta ERD may express inhibitory information processing throughout these loops. During the STM delay period, the prominent theta ERD was possibly related to focus on circumscribed memorization processes by the inhibition of concomitant irrelevant processes. An intriguing speculation is that cortical theta oscillations characterize the selective memorization processes induced by delayed choice reaction time (Bastiaansen et al., 2002) respect to the massive memorization processes occurring

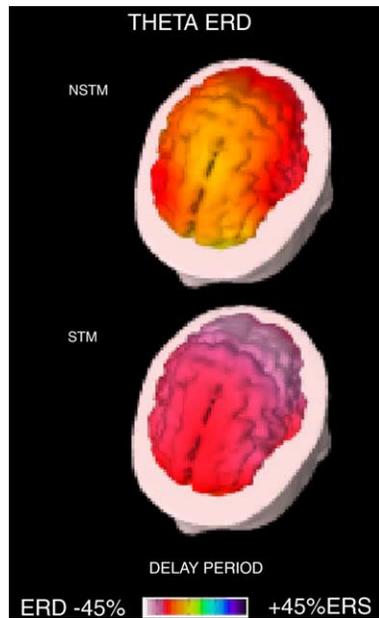


Fig. 6. Three-dimensional color maps of group theta ERD peak for the NSTM and the STM tasks. Color scale: maximum ERD and ERS are coded in white and violet, respectively. The maximal (%) value of the ERD/ERS is reported.

when some distractors intermingle the cue and probe stimuli to be matched ('n-back tasks'; [Gevins et al., 1997](#); [Gevins and Smith, 2000](#); [McEvoy et al., 2001](#)). This speculation merits to be experimentally tested manipulating the amount and type of the memory load with these diverse STM paradigms.

4.2. Alpha ERD is modulated by a very simple STM load

Despite the one-bit memory load, the STM condition did induce a prominent alpha ERD during the delay period when compared to the NSTM condition. The low alpha ERD (6–8 Hz) prevailed in bilateral frontal and left parietal areas, while the high alpha ERD (10–12 Hz) was maximal in the left fronto-parietal areas. According to the current view ([Klimesch, 1999](#)), the low alpha ERD would denote an enhancement of the attentional processes accompanying the STM. In parallel, the high alpha ERD would unveil an enhancement of task-specific STM processes. On the whole, the bilateral distribution of the alpha ERD could suggest that the coding and rehearsal of visuospatial representations mainly impinge upon right posterior areas ([Smith and Jonides, 1997](#)), whereas left frontal and parietal areas could support a possible complementary verbalization in encoding, storage, and rehearsal processes ([Fiez and Petersen, 1998](#)). Of course, the explanation of the alpha ERD topography in terms of either visuospatial, phonological or somatomotor coding of the task is rather opportunistic. It would require further experiments manipulating the contents to be memorized.

The present alpha ERD could not dissociate the two main processes occurring during the delay period, namely the retention and the motor preparation ([Rowe et al., 2000](#)). However, the motor preparation may not confound the results for at least 3 reasons. First of all, the motor preparation was paired for the NSTM and STM conditions, in which the time intervals, go stimulus, and motor demands were identical. Secondly, the delay period between the cue and go stimuli varied trial-by-trial (3.5–5.5 s), to discourage

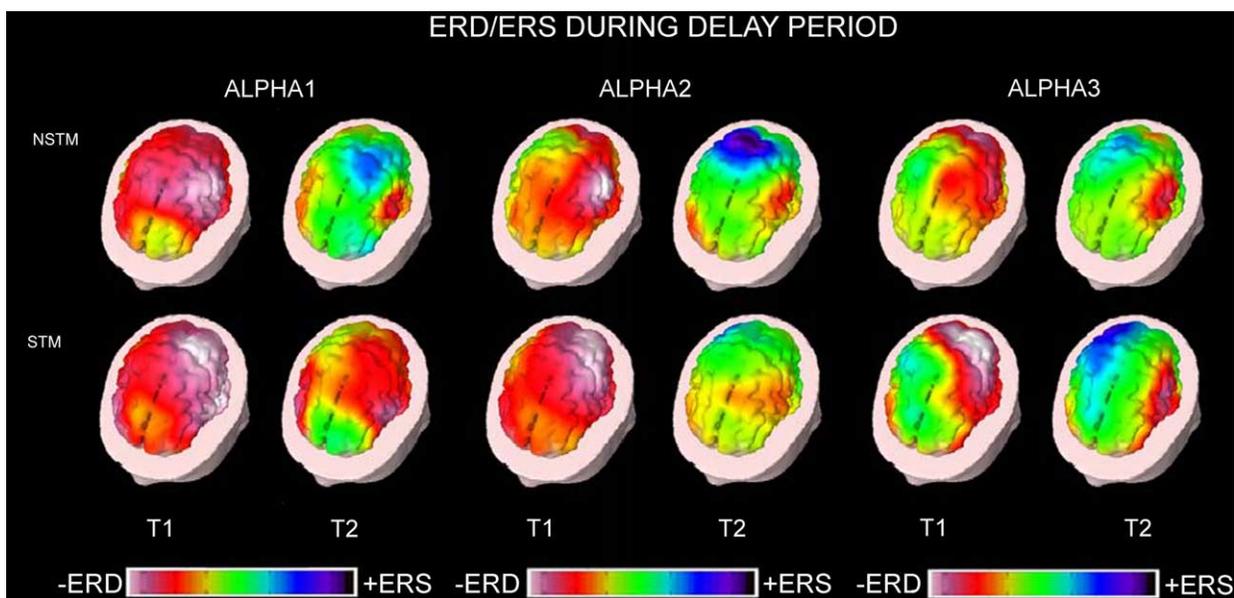


Fig. 7. Three-dimensional color maps of group alpha 1, alpha 2 and alpha 3 ERD peak (T1) and ERS peak (T2) during the delay period of the NSTM and STM conditions. Color scale as in [Fig. 6](#). The maximal ERD/ERS values were $\pm 34\%$ for the alpha 1, $\pm 45\%$ for the alpha 2, and $\pm 42\%$ for the alpha 3.

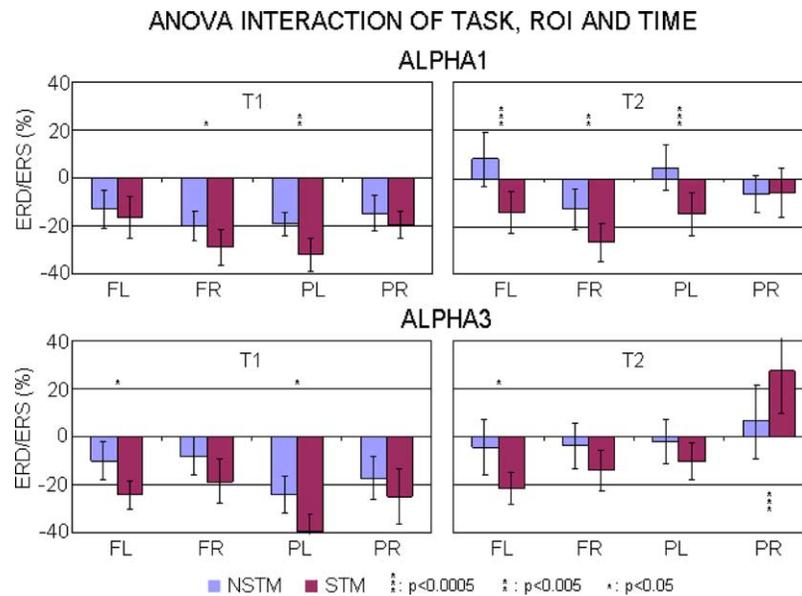


Fig. 8. Across subject means (\pm standard error) of the ERD/ERS amplitudes as provided by the ANCOVA design (movement reaction time as a covariate). In particular, these means refer to a statistical interaction among the factors Condition (NWM, WM), Region of interest (left frontal, right frontal, left parietal, right parietal), and Time period (ERD peak or T1, ERS peak or T2). The alpha 1 (top) and alpha 3 (bottom) ERD/ERS values were used as dependent variables. The results of Duncan post hoc testing are indicated by asterisks.

a pre-stimulus motor preparation. Thirdly, the alpha ERD reduced (ERS) rather than increased during the delay period. Notably, the typical trend of the motor preparation is a progressive increase of the alpha ERD up to the movement execution (Hari et al., 1997; Pfurtscheller and Lopes da Silva, 1999). Therefore, it is more probable that the present alpha ERD depended on the retention processes, in accordance with previous evidence showing that the alpha ERD does not differ during the delay period followed by hand vs. eye movements (Okada and Salenius, 1998).

The present results extend those of a recent low-resolution EEG study on delayed reaction time tasks in which low but not high alpha ERD has been reported (Bastiaansen et al., 2002). In that previous study (Bastiaansen et al., 2002), the warning (100 ms) and cue (150 ms) stimuli were very short, leading to a visual evoked response even during the delay period. Consequently, this visual evoked potential characterized by synchronization of alpha band could mask parallel alpha ERD occurring during the delay period. On the other hand, the present results complement previous high-resolution EEG evidence during 'n-back' tasks showing an alpha ERD in two sub-bands. It has been reported that the low alpha ERD (8–10 Hz) was equally modulated by the STM of both spatial and verbal stimuli (Gevins et al., 1997), in agreement with the notion that the low alpha is mainly related to attentional processes (Pfurtscheller and Lopes da Silva, 1999; Klimesch, 1999). In contrast, the high alpha (10–12 Hz) presented a reduction in magnitude in posterior parietal and occipital areas, which was stronger with heavy memory load (Gevins et al., 1997; Gevins and Smith, 2000; McEvoy et al., 2001). The present evidence of high alpha ERD during the delay period is also

in agreement with the findings of whole-head MEG recordings (Okada and Salenius, 1998) and with the notion that it mainly reflects task-specific processes (Pfurtscheller and Lopes da Silva, 1999; Klimesch, 1999).

An alternative explanation of the present findings is that the alpha ERD depended on the visual stimulation rather than on the memorization processes. Such an explanation is based on a previous MEG study (Okada and Salenius, 1998) in which alpha ERD differed between NSTM and STM conditions. However, the same differences were observed when subjects actively performed the tasks vs. passively fixed the screen. The conclusion was that the alpha ERD differences were independent of the memorization processes. Here we used long warning (1 s) and cue (2 s) stimuli in order to avoid or minimize during the delay period the effects of a physiological visual evoked potential after the visual stimuli during the delay period. As a consequence, visual processes as revealed by the visual evoked potentials ended before the delay (memorization) period. Furthermore, two considerations make it improbable the alternative explanation. Firstly, substantial visual processes during the NSTM delay period (prolonged cue stimulus) would have caused an alpha ERD stronger during the NSTM than STM condition. In contrast, the alpha ERD was stronger and longer during the STM than NSTM condition. Secondly, substantial visual processes during the STM delay period ('blank screen') would have caused an alpha ERD stronger over bilateral parietal areas, given that the visual stimulation was delivered over the whole subject's visual field. This was not the case. Compared to the NSTM condition, the STM condition induced a prevalence of left parietal alpha ERD.

5. Conclusions

This high-resolution EEG study in young adults showed the fronto-parietal theta and alpha ERD/ERS during the lowest STM load, as that induced by a delayed choice reaction time task. Compared to the control condition, the theta power (4–6 Hz) decreased in left frontal and bilateral parietal areas (delay period). Furthermore, the low alpha power (6–8 Hz) decreased in bilateral frontal and left parietal areas, while the high alpha power (10–12 Hz) decreased in the left fronto-parietal areas. The decrease of the alpha power is as an expression of the efficient information transfer within thalamo-cortical pathways. In conclusion, even a very simple STM task (only one bit to be memorized) revealed changes in fronto-parietal theta and alpha rhythms, which might probe progressive cortical responses associated with physiological and pathological aging.

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