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Research Report

Brain oscillatory 4–30 Hz responses during a visual *n*-back memory task with varying memory load

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A R T I C L E   I N F O

A B S T R A C T

Brain oscillatory responses of 4–30 Hz EEG frequencies elicited during the performance of a visual *n*-back task were examined in 36 adult volunteers. Event-related desynchronization (ERD) and event-related synchronization (ERS) responses were examined separately for targets and non-targets in four different memory load conditions (0-, 1-, 2- and 3-back). The presentation of all stimuli in all memory load conditions elicited long-lasting theta frequency (~4–6 Hz) ERS responses which were of greater magnitude for the target stimuli as compared to the non-target stimuli. Alpha frequency range (~8–12 Hz) ERD responses were observed in all memory load conditions for both targets and non-targets. The duration of these alpha ERD responses increased with increasing memory load and reaction time. In all memory load conditions, early appearing beta rhythm (~14–30 Hz) ERD responses were elicited, and with increasing memory load, these beta ERD responses became longer in duration. Additionally, beta ERS responses were observed in the 0- and 1-back memory load conditions. The current results reveal a complex interplay between brain oscillations at different frequencies during a cognitive task performance.

1. Introduction

Working memory can be considered as a cluster of dynamic modules (a central executive with slave systems, such as a phonological loop and a visuospatial sketchpad) operating on a time scale of seconds (Baddeley, 1986, 2003). Working memory is necessary for "online" information processing and information storage needed for complex cognitive processing, such as language comprehension, learning and reasoning (Baddeley, 1986, 2003). Cognitive processing requires the transient integration of numerous, widely distributed, constantly interacting areas of the brain (Basar, 2005; Basar et al., 2001a; Fuster, 2000; Klimesch, 1996; Ward, 2003). It has been

proposed that such complex cognitive processes could be implemented by synchronization of neurons into transient oscillatory assemblies (Singer, 1999; Varela et al., 2001), i.e., the formation of dynamic links mediated by neuronal synchrony. Such neuronal synchrony (or desynchrony) can be assessed by means of scalp recorded electroencephalogram (EEG).

The EEG signal can be decomposed into oscillatory components of different frequencies and the wavelet analysis method allows for the inspection of the EEG signal simultaneously as a function of time and frequency (e.g., in Basar et al., 2001b). It is now acknowledged that human scalp recorded EEG oscillatory responses at different frequencies can be related to several aspects of cognitive functioning ranging

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from stimulus processing, attention, working memory to long-term memory (Basar et al., 1999, 2001a; Klimesch, 1999; Ward, 2003). For example, increased theta frequency range (~3–8 Hz) oscillatory responses have been reported in association with working memory functions (see e.g., Bastiaansen and Hagoort, 2003; Kirk and Mackay, 2003; Klimesch, 1996; Rizzuto et al., 2003), responding to e.g., memory load (Jensen and Tesche, 2002) and task demands (Gevins et al., 1997; Raghavachari et al., 2001). Also target stimulus detection has been reported to be associated with increased theta responses (Klimesch et al., 2000; Mazaheri and Picton, 2005). Event-related responses of the alpha frequencies (~6–12 Hz) have been related to e.g., attention, alertness (Klimesch et al., 1998) and memory processes (Klimesch, 1999; Krause et al., 1996; Krause et al., 1999). Typically, increased cognitive load is associated with decreases in alpha power (Gevins et al., 1997; Krause et al., 2000; Stipacek et al., 2003). The responses of the beta frequencies (~20 Hz) were first associated with the activity of the motor cortices in relation to movement (Pfurtscheller et al., 1998; Stancak and Pfurtscheller, 1996), movement planning (Alegre et al., 2003; Kaiser et al., 2001) and motor imagery (Pfurtscheller and Neuper, 1997). Recently, beta rhythm responses have been reported also in association with cognitive processing (Karrasch et al., 2004; Kopp et al., 2004; Pesonen et al., 2006; Tallon-Baudry, 2003; Weiss and Rappels-berger, 1998).

Event-related oscillatory EEG responses can be quantified e.g., by means of the event-related desynchronization method (ERD) (Pfurtscheller and Aranibar, 1977; Pfurtscheller and Lopes da Silva, 1999). In this method, a relative decrease in the power of a certain frequency band during stimulus processing (as compared to a no-stimulation reference) is called event-related desynchronization (ERD), whereas the opposite, a relative increase in the power is called event-related synchronization (ERS) (Pfurtscheller and Lopes da Silva, 1999). The ERD/ERS values are within-subject measures of relative changes in the EEG (Krause, 2003; Pfurtscheller and Lopes da Silva, 1999). As is the case with the EEG, also the ERD/ERS technique is characterized by a relatively good temporal resolution and provides a suitable method to assess dynamic brain oscillatory responses during cognitive processing.

In cognitive neuroscience, one widely used experimental paradigm in studies of working memory is the so-called n-back task, in which the subjects are instructed to monitor a sequence of stimuli and to respond whether a stimulus presented is the same as the one presented n trials previously (where n is a pre-specified integer, varying usually from 0 to 3). During the performance of this working memory task the stimuli are sequentially registered and stored, and the task performance requires continuous updating of stimulus information. The increase of memory load in the n-back task is typically witnessed on the behavioral level as increased reaction times and as enhanced number of incorrect responses.

Reports on brain oscillatory responses during the performance of the n-back task are hitherto scarce. In year 2000, Krause et al. reported of brain oscillatory (ERD/ERS) responses of the 4–12 Hz EEG frequencies during a visual n-back task utilizing the 0-, 1- and 2-back memory load conditions (Krause et al., 2000). In that study, the ERD/ERS responses of the theta frequencies (4–6 Hz) were found to dissociate between targets and non-targets such that these responses were greater for the target stimuli. In contrast, the ERD/ERS responses of the alpha frequencies (8–12 Hz) distinguished between the different memory load conditions such that the alpha ERD responses were of greatest magnitude and of longest duration in the highest memory load condition (Krause et al., 2000).

The aim of the current study was to evaluate the human brain oscillatory response system associated with cognitive processing by means of assessing the ERD/ERS responses of the 4–30 Hz EEG frequencies during a visual working memory task with four memory load conditions. Thus, we partially replicated the study by Krause et al. (2000), however, using four memory load conditions (as compared to the three levels in the year 2000 study). In addition, in the current study we analyzed the responses of a broad EEG frequency band (4–30 Hz) as a function of time (0–1800 ms) and for five electrode sites. This experimental and analysis setting allowed us to make more detailed observations on the brain oscillatory system during working memory processing.

2.   Results

The behavioral results (mean RTs and percentages of correct answers) are displayed in Table 1.

As can be seen from Table 1, the reaction times increased and the number of correct responses decreased with increasing memory load. Due to these observations, the main effect for the factor LOAD was statistically significant on both reaction times ($F(1.168, 40.9) = 34.1$, $p < 0.001$) and percentages of correct answers ($F(1.83, 64.1) = 56.175$, $p < 0.001$).

The statistically significant ($p < .01$) mean ERD/ERS values for the four memory load conditions (0-, 1-, 2- and 3-back), separately for the non-target and target stimuli and for the five electrode locations, are displayed in Fig. 1 (in A) for the non-targets and (in B) for the targets. In addition, in Fig. 1, the statistically significant differences ($p < 0.01$) between the ERD/ERS responses elicited in different memory load conditions (in C) for the non-targets and (in D) for the targets and between the ERD/ERS responses elicited for the target and non-target stimuli (E) are presented.

As can be seen in Fig. 1, in general, ~4–6 Hz ERS responses were elicited at 0–1800 ms in all memory load conditions for both targets and non-targets. Higher frequency (~14–23 Hz) ERS responses were witnessed only in the 0- and 1-back memory load conditions at ~500–1800 ms. As a function of

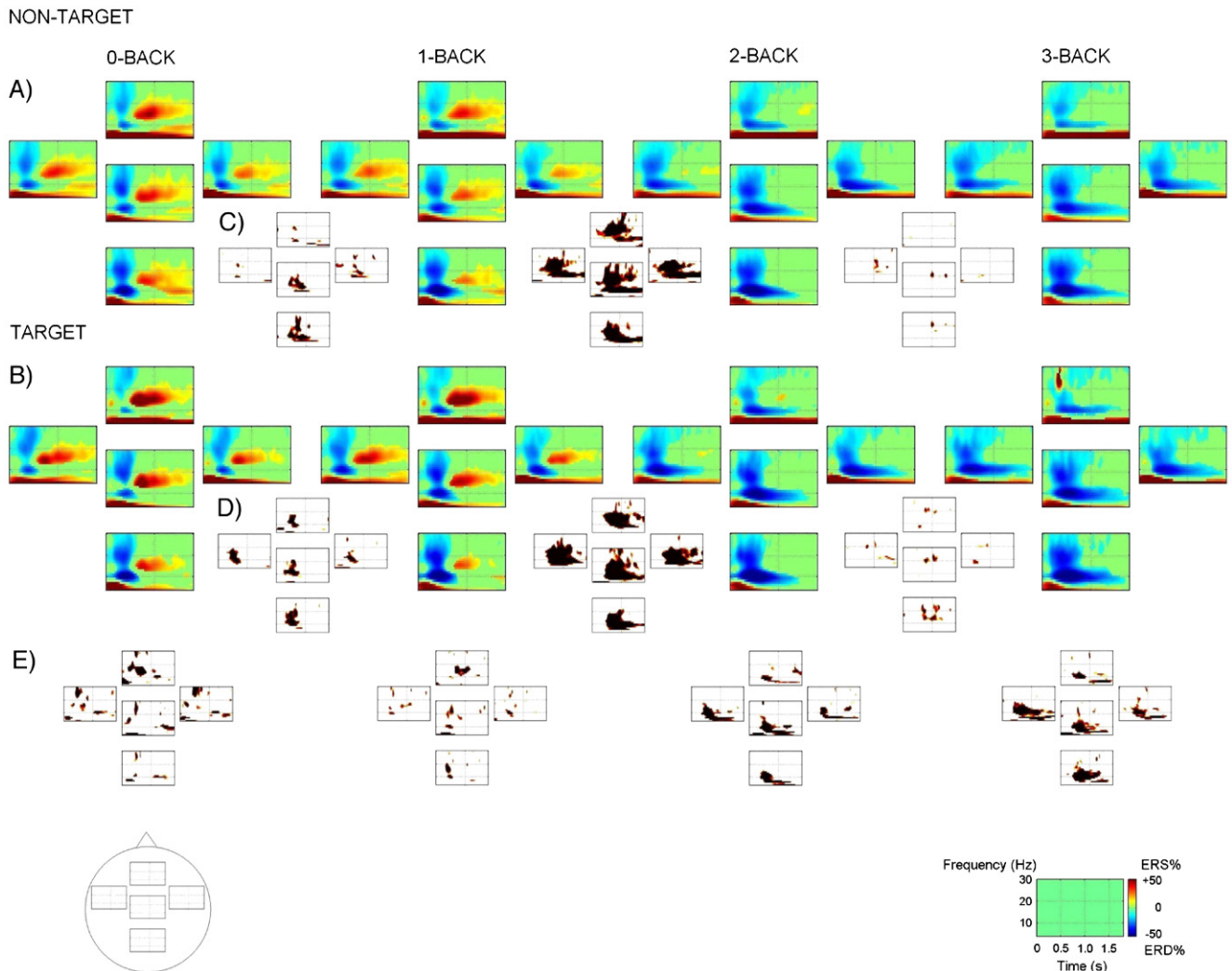| Table 1 – Mean (SD) reaction times (s) and percentages of correct answers for the four different memory load conditions				
Memory load condition	0-back	1-back	2-back	3-back
Correct responses % (SD)	98.71 (1.00)	96.95 (1.90)	96.08 (2.72)	92.55 (4.13)
Reaction time (s) (SD)	0.432 (0.105)	0.514 (0.164)	0.832 (0.450)	1.344 (0.924)

Fig. 1 – Statistically significant (*p*<.01) mean ERD/ERS values and results of the statistical analyses. In each TFR (time–frequency representation), the *y*-axis depicts frequencies (4–30 Hz) and the *x*-axis represents time (0–1800 ms) from stimulus onset (the scale presented in lower right corner). The TFRs are displayed for five electrode locations: frontal, left temporal, centro-parietal, right temporal and occipital regions. The locations are presented nose up (see lower left corner). The first row (A) illustrates the statistically significant (*p*<0.01) mean ERD/ERS values elicited during non-target stimulus presentation and the second row (B) depicts the statistically significant (*p*<0.01) mean ERD/ERS values elicited during target stimulus presentation. The results are depicted for all four memory load conditions. Blue colors denote ERD and red colors denote ERS, ranging from −50% to 50% (the scale presented in lower right corner). Green color denotes non-significant points. The statistically significant (*p*<0.01 marked with brown colors) differences between 0- vs. 1-back, 1- vs. 2-back, and 2- vs. 3-back memory load conditions are depicted (in panel C) for the non-target stimuli and (in panel D) for the target stimuli. The probability TFRs are placed between the memory load conditions compared. Additionally, the statistically significant (*p*<0.01 marked with brown colors) differences between non-target and target stimuli within each memory load condition are displayed in a row (E).

memory load, temporally varying ERD responses were elicited in the ~8–12 Hz and ~14–30 Hz frequencies.

Theta ERS responses: The presentation of all visual stimuli elicited long-lasting (0–1800 ms) theta (~4–6 Hz) ERS responses. The magnitude of these responses was statistically significantly of greater magnitude for the target stimuli than for the non-target stimuli, especially in the parietal recording sites.

Alpha ERD responses: Statistically significant alpha frequency range (~8–12 Hz) ERD responses were observed in all memory load conditions for both targets and non-targets beginning at ~100 ms after visual stimulus onset. The duration of these alpha ERD responses increased with increasing memory load, being ~100–500 ms in the 0-back and ~100–1600 ms in the 3-back memory load condition. The magnitude of these alpha ERD responses in the 2- and 3-back memory load conditions was statistically significantly of greater magnitude for the targets as compared to the non-targets.

Beta ERD responses: In all memory load conditions, early appearing beta rhythm (~14–30 Hz) ERD responses were elicited with an onset at ~100 ms. With increasing memory load, these beta rhythm ERD responses became longer in

duration. Significant differences between the magnitude of these beta ERD responses between the targets and non-targets arose in the 2- and 3-back memory load conditions, such that greater beta ERD was observed for the targets than for the non-targets (~10–18 Hz).

Beta ERS responses: Only in the 0- and 1-back memory load conditions, ~14–23 Hz frontal ERS responses were observed approximately at ~500–1800 ms after visual stimulus onset. These ERS responses were of greater magnitude for the target stimuli as compared to non-targets, which effect was witnessed especially in the frontal electrodes.

3.   Discussion

In the current study, we assessed brain oscillatory EEG ERD/ERS responses elicited during a visual *n*-back task performance. We thus partially replicated an earlier study by Krause et al. (2000). The ERD/ERS responses of a broad EEG frequency band (4–30 Hz) and five electrode sites were analyzed as a function of time (0–1800 ms). Also behavioral reaction time and task performance data were recorded and analyzed.

As expected, on the behavioral level, both the percentage of incorrect answers and reaction times increased with increasing memory load.

The presentation of all stimuli in all memory load conditions elicited long-lasting (0–1800 ms) theta (~4–6 Hz) ERS responses. This finding is in line with the previous report of Krause et al. (2000), in which similar long-lasting ERS responses were witnessed in the 4–6 Hz theta frequency range in all memory load conditions. Theta ERS responses have previously been reported in association with memory encoding and retrieval both in the visual and auditory stimulus modality (Jensen and Tesche, 2002; Karrasch et al., 2004; Klimesch et al., 2001, 2005; Krause et al., 2000; Pesonen et al., 2006) and such theta ERS responses may be associated with working memory processes and, more specifically, with the functioning of the central executive (Baddeley, 1986, 2003; Klimesch et al., 2005; Sauseng et al., 2005). We propose that the long-lasting theta ERS responses observed in the current study may reflect the continuous cognitive processing (information maintenance and manipulation) required in the performance of the *n*-back task. However, these theta ERS responses systematically dissociated between the target and non-target stimuli, being always of greater magnitude for the target stimuli as compared to the non-target stimuli. This observation supports the assumption that stimulus recognition (target identification) processes are reflected as increased responses in the EEG theta response system (Klimesch et al., 2000; Krause et al., 2000; Mazaheri and Picton, 2005).

In line with the year 2000 report (Krause et al., 2000), also in the current study, alpha frequency range (~8–12 Hz) ERD responses were observed in all memory load conditions for both targets and non-targets, and the duration of these alpha ERD responses became steadily longer with increasing memory load. Our current observations bespeak for the assumption according to which alpha ERD responses are closely associated with memory processing, especially to memory load and memory demands (Gevins et al., 1997; Krause et al., 2000; Stipacek et al., 2003).

The earlier study by Krause et al. (2000) examined the ERD/ERS responses of narrow theta and alpha EEG frequency bands and reported that the responses of the 8–10 and 10–12 Hz alpha frequencies differed as a function of memory load. In the current study, no such narrow frequency alpha EEG effects were observed. Instead, the alpha frequency band responding to memory load was broad (~8–12 Hz) and became broader with increasing memory load. In fact, in the 2- and 3-back memory load conditions, the alpha ERD responses became almost indistinct from the higher frequency (~14–30 Hz) ERD responses. Such discrepancies between the year 2000 study and the current data may at least partially be explained by the different EEG signal analysis methodologies. However, from both studies we conclude that the alpha frequency response system dynamically responds to working memory demands (memory load) such that increased alpha ERD responses emerge with increasing memory demands. The results of the current study also indicate a relationship between the duration of the alpha ERD responses and the reaction times, suggesting a relationship between cognitive processing, behavior and the alpha response system.

In all memory load conditions, early appearing higher frequency beta rhythm (~14–30 Hz) ERD responses were elicited beginning at ~100 ms. Event-related brain oscillatory responses in the beta frequency range were first associated with the activity of the motor cortices (Alegre et al., 2003; Kaiser et al., 2001; Pfurtscheller and Neuper, 1997; Pfurtscheller et al., 1998; Stancak and Pfurtscheller, 1996), but recently beta rhythm responses have also been reported in association with cognitive processing (see e.g., Karrasch et al., 2004; Kopp et al., 2004; Pesonen et al., 2006; Tallon-Baudry, 2003; Weiss and Rappelsberger, 1998). This early beta rhythm ERD may at least partially reflect the activity of the motor cortices, i.e., the preparation of the motor response required as soon as possible after each stimulus identification/recognition. These beta rhythm ERD responses became longer with increasing memory load, which may be associated with the simultaneous increases in reaction times. However, it should be noted that recently beta rhythm ERD responses have been reported in association with cognitive tasks in which no immediate motor response has been required (Bastiaansen et al., 2005; Karrasch et al., 2004, 2006; Pesonen et al., 2006). Only modest, and only in the 2- and 3-back memory load conditions, differences arose in these beta ERD responses between the targets and non-targets, such that greater beta ERD was witnessed for target stimuli than for non-target stimuli (~10–18 Hz). Thus, the beta frequency ERD responses did not differentiate between targets and non-targets to the same extent as the ERS responses of the theta frequencies. To which extent the beta ERD responses witnessed in the current study are related to motor planning and/or cognitive/memory processing needs to be clarified in separate studies, specifically focusing on this question.

Beta frequency ERS responses were observed, but in the 0- and 1-back memory load conditions only, emerging after the initial beta ERD responses (see above). The responsive frequency band of these beta ERS responses was narrower (~14–23 Hz) than the corresponding beta ERD frequency band (~14–30 Hz). Whereas the beta rhythm ERD responses were most pronounced in the posterior recording sites, the beta ERS

responses were greatest in the frontal electrodes. Such spatial differences between the beta ERD and ERS responses may suggest the presence of two distinct beta response systems. We suggest that the beta ERS responses (witnessed only in the 0- and 1-back memory load conditions) may be related to the activity of the motor cortices (Alegre et al., 2003; Kaiser et al., 2001; Labyt et al., 2003; Pfurtscheller and Neuper, 1997), more specifically to the post-movement "beta-rebound" (Pfurtscheller et al., 1998, 2003; Stancak and Pfurtscheller, 1996). Such post-movement beta rhythm ERS responses may not be observed in the mean ERD/ERS values in the 2- and 3-back memory load conditions because of the lengthening of the reaction times and increased variance in the timing of the responses. However, the obvious difference in these beta rhythm ERS responses between the 0- & 1- vs. the 2- & 3-back memory load conditions may also suggest some relationship between these ERS responses and cognitive strategy as the performance of the 2- and 3-back conditions requires increases in memory maintenance, rehearsal and attentional resources as compared to the 0- and 1-back conditions (Cohen et al., 1997; Honey et al., 2002; Jonides et al., 1997; Krause et al., 2000; Ross and Segalowitz, 2000). Also the fact that these beta rhythm ERS responses dissociated between the target and non-target stimuli, however in the 0- and 1-back memory load conditions only, may reflect at least some roles of beta rhythm oscillations in cognitive processing. Also this question must be addressed in future studies in which the cognitive task and the motor responses must be systematically modified, controlled for and related to the beta rhythm responses.

We conclude that cognitive processes involve highly complex patterns of brain oscillations at different frequencies, and the results from the current study express this complexity. Compound patterns of theta, alpha and beta rhythm oscillatory responses emerge during cognitive processing.

4. Experimental procedures

Thirty six healthy male volunteers participated in the experiment (mean age = 22.9 years, SD = 2.37, range 18–27 years). All participants were right-handed native speakers of Finnish with normal or corrected vision. None of the participants reported any neurological disorders.

The experimental design was a visual sequential letter memory task (n-back task) with varying memory load from 0-back to 3-back. The visual stimuli were pseudorandom sequences of letters (randomly varying in case), presented white on black background. The participants observed stimuli on a visual display and responded using a hand-held response pad. In the 0-back condition, participants responded to a single pre-specified target letter ("X"). In the 1-back condition, the target was any letter identical to the immediately preceding one (i.e., one trial back). In the 2-back condition, the target was any letter that was presented two trials back, and in the 3-back condition, the target was any letter which was presented three trials back. Thus, working memory load was varied from 0 to 3 items. Stimulus was present on the screen until participant responded, and after the response with 2500 ms ISI (inter-stimulus interval) the next stimulus was presented. Participants responded to each stimulus by pressing a button with their right hand, with middle finger for targets and with index finger for non-targets. Reaction times to responding were recorded. The visual stimuli were generated and presented using NeuroScan STIM software.

The participant was seated in a comfortable chair in the EEG registration room and the experimental procedure was explained. In order to reduce muscle artifacts in the EEG signal, the participant was instructed to assume a comfortable position and to avoid movement. The participant was instructed to look at a TV screen placed in front of him (1.6 m) and to avoid unnecessary eye movements. The participants were instructed to respond as fast and as accurately as possible to each stimulus by pressing one button for targets and another for non-targets. The participants' responses were monitored (reaction times and correct responses) and only trials with correct responses were included in the EEG analysis. The length of a single memory load experimental condition was 10 min (+ response time) and there were 120 trials in each memory load experimental condition. Each task with different memory load condition was performed twice. The order of the four memory load conditions was counterbalanced between the participants.

The EEG data were gathered from 19 electrodes by using Electro-Cap (Electro-Cap International Inc.) with the international 10/20 system of electrode placement. Additionally, two EOG electrodes were placed on the outer sides of eyes and all electrodes were referred to right mastoid electrode. Electrode attached to the middle of the head was serving as ground electrode. The EEG data were recorded using Neuroscan 386 Scan 4.1 data acquisition system with a SynAmps amplifier with a frequency band of 0.1–50 Hz and sampled at 250 Hz. The impedance of recording electrodes was monitored and kept always below 5 kΩ.

The digitalized EEG data were processed in a MATLAB® 6.5 environment (MathWorks Inc.) using modifications of the 4-D Toolbox (Jensen, 2002) scripts. The data were processed to time–frequency representations (TFRs), which display the power of EEG signal as a function of time and frequency in the same matrix. The calculations were performed for each EEG channel separately. Artifact rejection was set to ±100 μV. Poor quality signal channels were excluded from further analyses by means of visual inspections of the TFRs displaying the absolute power values.

Time–frequency representations for each participant and for each event (presentation of target/non-target stimuli in each memory load condition) were calculated using a Morlet wavelet (width 8) for EEG frequencies 4–30 Hz. The EEG data were epoched using a time window of 2600 ms for the stimuli, and the reference was epoched using a time window of 1000 ms prior to each stimulus presentation and was averaged over time. The TFRs for the events and the reference were averaged separately for each participant. Thereafter, the relative difference in the power of EEG between the reference and the stimulus presentation (target/non-target) was calculated as a function of time and frequency. The difference was expressed as ERD/ERS percentage in which negative values indicate relative power decrease (ERD) and positive values indicate relative power increase (ERS). The averaged ERD/ERS TFRs were calculated for both stimulus types, targets and non-targets, in all four memory load conditions. The ERD/ERS TFRs

were displayed for five electrode locations (frontal Fp1 Fp2 F3 Fz F4, left temporal F7 T3 C3 T5, right temporal F8 T4 C4 T6, parietal Cz P3 Pz P4, occipital O1 O2) as a function of time (0–1800 ms) and frequency (4–30 Hz).

The nonparametric Quade test (Quade, 1979) was used to assess the statistical significance of the ERD/ERS responses per se. The results were displayed as TFRs, in which only statistically significant ERD/ERS responses were shown as a function of frequency and time. Statistically significant differences between memory load conditions for target and non-target stimuli were assessed pair-wise (0- vs. 1-back, 1- vs. 2-back, and 2- vs. 3-back) using the same statistical test. Additionally, the significance of any differences between the ERD/ERS responses elicited by targets and non-targets within each memory load condition was assessed. The results of the statistical tests were displayed in probability TFRs in which the statistically significant differences were illustrated as a function of time and frequency. The statistical computations were performed in the MATLAB® 6.5 environment (Math-Works Inc.).

The reaction times (RT) and the number of correct responses to the task were recorded for each memory load condition. The statistical significance of the differences in the RTs and the percentages of correct answers between the memory load conditions were analyzed using a repeated measures analysis of variance (ANOVA) with one within-subjects factor LOAD (four levels: 0-back, 1-back, 2-back and 3-back). Factors with three or more levels carry an assumption known as sphericity or circularity (Vasey and Thayer, 1987). Violation of this assumption results in positively biased tests. One method to compensate for this bias is to adjust the degrees of freedom using the Greenhouse–Geisser procedure. When appropriate, this procedure was used to compensate for non-sphericity. Corrected degrees of freedom and corrected p-values are displayed for the behavioral results.

Acknowledgments

R E F E R E N C E S

Alegre, M., Labarga, A., Gurtubay, I.G., Iriarte, J., Malanda, A., Artieda, J., 2003. Movement-related changes in cortical oscillatory activity in ballistic, sustained and negative movements. Exp. Brain Res. 148, 17–25.
Baddeley, A., 1986. Working Memory. Oxford University Press, New York.
Baddeley, A., 2003. Working memory: looking back and looking forward. Nat. Rev., Neurosci. 4, 829–839.
Basar, E., 2005. Memory as the "whole brain work": a large-scale model based on "oscillations in super-synergy". Int. J. Psychophysiol. 58, 199–226.
Basar, E., Basar-Eroglu, C., Karakas, S., Schurmann, M., 1999. Are cognitive processes manifested in event-related gamma, alpha, theta and delta oscillations in the EEG? Neurosci. Lett. 259, 165–168.
Basar, E., Basar-Eroglu, C., Karakas, S., Schurmann, M., 2001a. Gamma, alpha, delta, and theta oscillations govern cognitive processes. Int. J. Psychophysiol. 39, 241–248.
Basar, E., Schurmann, M., Demiralp, T., Basar-Eroglu, C., Ademoglu, A., 2001b. Event-related oscillations are 'real brain responses'—Wavelet analysis and new strategies. Int. J. Psychophysiol. 39, 91–127.
Bastiaansen, M., Hagoort, P., 2003. Event-induced theta responses as a window on the dynamics of memory. Cortex 39, 967–992.
Bastiaansen, M.C., van der Linden, M., Ter Keurs, M., Dijkstra, T., Hagoort, P., 2005. Theta responses are involved in lexical-semantic retrieval during language processing. J. Cogn. Neurosci. 17, 530–541.
Cohen, J.D., Perlstein, W.M., Braver, T.S., Nystrom, L.E., Noll, D.C., Jonides, J., Smith, E.E., 1997. Temporal dynamics of brain activation during a working memory task. Nature 386, 604–608.
Fuster, J.M., 2000. Cortical dynamics of memory. Int. J. Psychophysiol. 35, 155–164.
Gevins, A., Smith, M.E., McEvoy, L., Yu, D., 1997. High-resolution EEG mapping of cortical activation related to working memory: effects of task difficulty, type of processing, and practice. Cereb. Cortex 7, 374–385.
Honey, G.D., Fu, C.H., Kim, J., Brammer, M.J., Croudace, T.J., Suckling, J., Pich, E.M., Williams, S.C., Bullmore, E.T., 2002. Effects of verbal working memory load on corticocortical connectivity modeled by path analysis of functional magnetic resonance imaging data. NeuroImage 17, 573–582.
Jensen, O., 2002. 4-D Toolbox.
Jensen, O., Tesche, C.D., 2002. Frontal theta activity in humans increases with memory load in a working memory task. Eur. J. Neurosci. 15, 1395–1399.
Jonides, J., Schumacher, E.H., Smith, E.E., Lauber, E.J., Awh, E., Minoshima, S., Koeppe, R.A., 1997. Verbal working memory load affects regional brain activation as measured by PET. J. Cogn. Neurosci. 9, 462–475.
Kaiser, J., Birbaumer, N., Lutzenberger, W., 2001. Event-related beta desynchronization indicates timing of response selection in a delayed-response paradigm in humans. Neurosci. Lett. 312, 149–152.
Karrasch, M., Laine, M., Rapinoja, P., Krause, C.M., 2004. Effects of normal aging on event-related desynchronization/synchronization during a memory task in humans. Neurosci. Lett. 366, 18–23.
Karrasch, M., Laine, M., Rinne, J.O., Rapinoja, P., Sinervä, E., Krause, C.M., 2006. Brain oscillatory responses to an auditory–verbal working memory task in mild cognitive impairment and Alzheimer's disease. Int. J. Psychophysiol. 59, 168–178.
Kirk, I.J., Mackay, J.C., 2003. The role of theta-range oscillations in synchronising and integrating activity in distributed mnemonic networks. Cortex 39, 993–1008.
Klimesch, W., 1996. Memory processes, brain oscillations and EEG synchronization. Int. J. Psychophysiol. 24, 61–100.
Klimesch, W., 1999. EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis. Brain Res. Brain Res. Rev. 29, 169–195.
Klimesch, W., Doppelmayr, M., Russegger, H., Pachinger, T., Schwaiger, J., 1998. Induced alpha band power changes in the human EEG and attention. Neurosci. Lett. 244, 73–76.
Klimesch, W., Doppelmayr, M., Schwaiger, J., Winkler, T., Gruber, W., 2000. Theta oscillations and the ERP old/new effect: independent phenomena? Clin. Neurophysiol. 111, 781–793.
Klimesch, W., Doppelmayr, M., Stadler, W., Pollhuber, D., Sauseng, P., Rohm, D., 2001. Episodic retrieval is reflected by a process

specific increase in human electroencephalographic theta activity. Neurosci. Lett. 302, 49–52.

Klimesch, W., Schack, B., Sauseng, P., 2005. The functional significance of theta and upper alpha oscillations. Exp. Psychol. 52, 99–108.

Kopp, F., Schroger, E., Lipka, S., 2004. Neural networks engaged in short-term memory rehearsal are disrupted by irrelevant speech in human subjects. Neurosci. Lett. 354, 42–45.

Krause, C.M., 2003. Brain electric oscillations and cognitive processes. In: Hugdahl, K. (Ed.), Experimental Methods in Neuropsychology. Neuropsychology and Cognition. Kluwer Academic Publishers, Boston, pp. 111–130.

Krause, C.M., Lang, A.H., Laine, M., Kuusisto, M., Pörn, B., 1996. Event-related EEG desynchronization and synchronization during an auditory memory task. Electroencephalogr. Clin. Neurophysiol. 98, 319–326.

Krause, C.M., Åström, T., Karrasch, M., Laine, M., Sillanmäki, L., 1999. Cortical activation related to auditory semantic matching of concrete versus abstract words. Clin. Neurophysiol. 110, 1371–1377.

Krause, C.M., Sillanmäki, L., Koivisto, M., Saarela, C., Häggqvist, A., Laine, M., Hämäläinen, H., 2000. The effects of memory load on event-related EEG desynchronization and synchronization. Clin. Neurophysiol. 111, 2071–2078.

Labyt, E., Szurhaj, W., Bourriez, J.L., Cassim, F., Defebvre, L., Destee, A., Guieu, J.D., Derambure, P., 2003. Changes in oscillatory cortical activity related to a visuomotor task in young and elderly healthy subjects. Clin. Neurophysiol. 114, 1153–1166.

Mazaheri, A., Picton, T.W., 2005. EEG spectral dynamics during discrimination of auditory and visual targets. Brain Res. Cogn. Brain Res. 24, 81–96.

Pesonen, M., Haarala Björnberg, C., Hämäläinen, H., Krause, C.M., 2006. Brain oscillatory 1–30 Hz EEG ERD/ERS responses during the different stages of an auditory memory search task. Neurosci. Lett. 399, 45–50.

Pfurtscheller, G., Aranibar, A., 1977. Event-related cortical desynchronization detected by power measurements of scalp EEG. Electroencephalogr. Clin. Neurophysiol. 42, 817–826.

Pfurtscheller, G., Lopes da Silva, F.H., 1999. Event-related EEG/MEG synchronization and desynchronization: basic principles. Clin. Neurophysiol. 110, 1842–1857.

Pfurtscheller, G., Neuper, C., 1997. Motor imagery activates primary sensorimotor area in humans. Neurosci. Lett. 239, 65–68.

Pfurtscheller, G., Zalaudek, K., Neuper, C., 1998. Event-related beta synchronization after wrist, finger and thumb movement. Electroencephalogr. Clin. Neurophysiol. 109, 154–160.

Pfurtscheller, G., Woertz, M., Supp, G., Lopes da Silva, F.H., 2003. Early onset of post-movement beta electroencephalogram synchronization in the supplementary motor area during self-paced finger movement in man. Neurosci. Lett. 339, 111–114.

Quade, D., 1979. Using weighted rankings in the analysis of complete blocks with additive block effects. J. Am. Stat. Assoc. 74, 680–683.

Raghavachari, S., Kahana, M.J., Rizzuto, D.S., Caplan, J.B., Kirschen, M.P., Bourgeois, B., Madsen, J.R., Lisman, J.E., 2001. Gating of human theta oscillations by a working memory task. J. Neurosci. 21, 3175–3183.

Rizzuto, D.S., Madsen, J.R., Bromfield, E.B., Schulze-Bonhage, A., Seelig, D., Aschenbrenner-Scheibe, R., Kahana, M.J., 2003. Reset of human neocortical oscillations during a working memory task. Proc. Natl. Acad. Sci. U. S. A. 100, 7931–7936.

Ross, P., Segalowitz, S.J., 2000. An EEG coherence test of the frontal dorsal versus ventral hypothesis in n-back working memory. Brain Cogn. 43, 375–379.

Sauseng, P., Klimesch, W., Schabus, M., Doppelmayr, M., 2005. Fronto-parietal EEG coherence in theta and upper alpha reflect central executive functions of working memory. Int. J. Psychophysiol. 57, 97–103.

Singer, W., 1999. Neurobiology. Striving for coherence. Nature 397, 391–393.

Stancak Jr., A., Pfurtscheller, G., 1996. Event-related desynchronisation of central beta-rhythms during brisk and slow self-paced finger movements of dominant and nondominant hand. Brain Res. Cogn. Brain Res. 4, 171–183.

Stipacek, A., Grabner, R.H., Neuper, C., Fink, A., Neubauer, A.C., 2003. Sensitivity of human EEG alpha band desynchronization to different working memory components and increasing levels of memory load. Neurosci. Lett. 353, 193–196.

Tallon-Baudry, C., 2003. Oscillatory synchrony and human visual cognition. J. Physiol. (Paris) 97, 355–363.

Varela, F., Lachaux, J.P., Rodriguez, E., Martinerie, J., 2001. The brainweb: phase synchronization and large-scale integration. Nat. Rev., Neurosci. 2, 229–239.

Vasey, M.W., Thayer, J.F., 1987. The continuing problem of false positives in repeated measures ANOVA in psychophysiology: a multivariate solution. Psychophysiology 24, 479–486.

Ward, L.M., 2003. Synchronous neural oscillations and cognitive processes. Trends Cogn. Sci. 7, 553–559.

Weiss, S., Rappelsberger, P., 1998. Left frontal EEG coherence reflects modality independent language processes. Brain Topogr. 11, 33–42.