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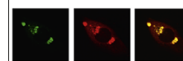Project   Attention, Negative Priming, BaseRates, Statistical Learning View project

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Research Report

Individual differences in working memory capacity are reflected in different ERP and EEG patterns to task difficulty

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ABSTRACT

This study examined whether there are neural markers of individual differences in working memory (WM) capacity and whether these differences are only manifest when performing a demanding WM task or at all levels of difficulty. Each subject's WM capacity was estimated using a modified digit span task prior to participation in an N-back task that varied difficulty from 1- to 4-back. While performing the N-back task, subjects wore scalp electrodes that allowed measurement of both event-related potentials (ERP) and event-related synchronization and desynchronization (ERS/ERD). Those subjects classified as low WM were more affected by the higher cognitive demands (many more errors in the 4-back task and generally slower responses) than those classified as high WM. These behavioral differences between the two groups were also apparent in the neural markers. Specifically, low WM subjects, when compared with high WM subjects, produced smaller P300 amplitudes and theta ERS, as well as greater alpha ERD at the most difficult level. Importantly, the observed differences in electrophysiological responses between the two groups were also observed at the lowest difficulty level, not just when the task challenged WM capacity. In addition, P300 amplitudes and alpha ERD responses were found to correlate with individual WM capacities independent of the task difficulty. These results suggest that there are qualitative neural differences among individuals with different WM capacities when approaching cognitive operations. Individuals with high WM capacities may make more efficient use of neural resources to keep their attention focused on the task-relevant information when performing cognitive tasks.

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1. Introduction

Working memory (WM) is a set of mechanisms involved in the temporary retrieval, maintenance, and manipulation of information for a wide range of cognitive operations (e.g., Baddeley, 1992, 2003). Individual differences in WM capacity have been shown to correlate with performance in a variety of tasks including learning, planning, comprehension and problem solving (Alloway, 2009; Conway, 1996; Engle, 1994) as well as with general fluid intelligence (Conway et al., 2002; Engle et al., 1999). Measures of WM capacity have also been shown to predict academic achievement better than measures of intelligence (Alloway and Alloway, 2010). Given the centrality of WM to human cognitive processing, it is important to better understand the nature of individual differences in WM capacity. Much of the earlier research employed paradigms such as the traditional digit span test (Dempster and Cooney, 1982), reading span task (Daneman and Carpenter, 1980) and operation span task (Conway, 1996; Turner and Engle, 1989) to explore individual differences in WM capacity and focused primarily on behavioral measures.

More recently, researchers have investigated WM effects within and between individuals using neuroimaging methods, relying extensively on the N-back paradigm both when employing functional magnetic resonance imaging (fMRI) (Braver et al., 1997; Jaeggi et al., 2007; Manelis and Reder, 2014; Owen et al., 2005) and event-related potentials (ERP) (Daffner et al., 2011; Gevins and Smith, 2000; McEvoy et al., 2001) studies. The N-back task requires that the subjects indicate whether the current stimulus is identical to the stimulus shown N presentations before. In a given block the value of N remains constant and blocks are more difficult the higher the value of N. For example, in the 1-back condition, subjects need only to hold the last item in WM, while the 2-back condition requires subjects to update two items to be held in WM as well as decide whether the item 2-back matches the current one. A reason for the popularity of this paradigm is that input and output aspects of the task do not vary with increased WM load. Specifically, the visual input (a sequential presentation of stimuli) and the nature of the response (one of two button presses) remain constant across values of N. Therefore, any differences in performance or neuroimaging measures across values of N can be attributed to differences in WM demands as opposed to differences in the visual display or nature of the response.

Parametric variations of difficulty in the N-back task have enabled researchers to investigate neural changes as a function of WM demands (Braver et al., 1997; Daffner et al., 2011; Jaeggi et al., 2007; McEvoy et al., 2001; Pesonen et al., 2007; Watter et al., 2001). However, there have been few studies that have examined whether load-dependent changes in neural responses vary across individuals that have been shown to have different WM capacities, with the exception of a recent ERP study by Daffner et al. (2011). In addition, previous neuroimaging studies using the N-back task have not gone beyond 3-back. There have been several behavioral studies that have gone as high as 4- and 5-back (Jaeggi et al., 2010; Juvina and Taatgen, 2007; Verhaeghen and Basak, 2005), but no neurophysiological recordings have examined performance at such a high load. The current study explored whether there were electrophysiological signatures of individual differences in WM capacity and whether these differences were only manifest when performing a highly demanding WM task or at all levels of difficulty. We recorded scalp electroencephalography (EEG) signals in order to measure both ERP and event-related synchronization/desynchronization (ERS/ERD) during performance of the N-back task that varied N from 1 to 4.

The ERS/ERD measure tracks task-related changes in the synchrony of underlying neural populations (Klimesch, 1999; Pfurtscheller and Lopes da Silva, 1999). While the high temporal resolution of ERP enables researchers to examine the time course of cognitive operations, the spectral EEG oscillation (represented by ERS/ERD) can provide information about the dynamics of functional network formation (Bastiaansen and Hagoort, 2003). There has been a number of studies that suggest both measures are correlated with attentional resource allocation, WM capacity and general cognitive abilities (Gevins and Smith, 2000; Grabner et al., 2004; McEvoy et al., 2001; Polich, 2007). In a review article, Polich (2007) demonstrated that the P300 component played a role in attentional resource allocation among concurrent operations. Gevins and Smith (2000) found that the P300 amplitudes are positively correlated with subjects' WM capacities and general cognitive abilities. They also examined brain oscillations and found this same positive correlation with individuals' WM capacities and cognitive abilities for the frontal theta ($\sim$3–7 Hz) ERS. Similarly, McEvoy et al. (2001) reported that theta ERS is greater in younger than older adults when performing the N-back task. Lee et al. (2005) proposed that theta oscillations might be responsible for regulating the activation of relevant information maintained in WM. Finally, while the theta ERS findings showed a positive correlation with larger WM capacity, Grabner et al. (2004) found that higher intelligence is associated with lower alpha ($\sim$8–12 Hz) ERD responses, reflecting more efficient brain functioning in those scoring high on intelligence tests.

To extend the findings from the above research, the current study examined the P300 ERP component and EEG oscillations in the low frequency band ($<$15 Hz, including both theta- and alpha-band oscillations), in particular focusing on how these measures differed for subjects with different WM capacities. The expectation is that subjects with higher WM, as compared with subjects classified as having lower WM capacity, will show better performance on behavioral measures, greater amplitudes for the P300, larger values of theta ERS and attenuated alpha ERD. This pattern of differences based on WM capacity is expected to be strongest at the more challenging level of the N-back task. Conceivably, neural signals at the high difficulty level may result from something other than individual differences in WM capacity, such as the subject's effort to seek various strategies (Jaeggi et al., 2007), or the low WM subject's inability to engage in such a difficult task. Therefore, we were interested in looking at whether differences in the electrophysiological response patterns would also be observed at the lowest difficulty level, which placed few demands on individuals' WM.

It is important to note that prior studies that have explored individual differences in WM tasks such as the N-back have classified subjects as high and low groups based on their performance in the task itself (e.g., Daffner et al., 2011; Jaeggi et al., 2007). To avoid this circularity problem, we used
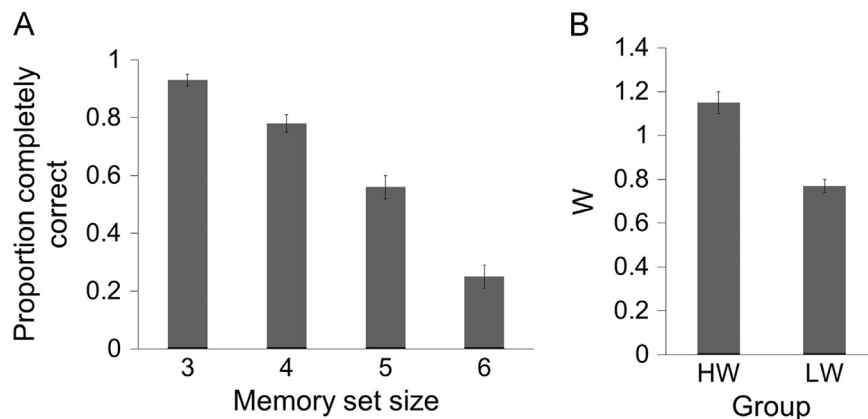
Fig. 1 – Behavioral results of the MODS task. **(A) Performance as a function of memory set size in the MODS task; (B) Mean estimated W values from the MODS task for the High and Low Working Memory Groups (HW and LW). The error bars in this and the following figures reflect one SEM.**
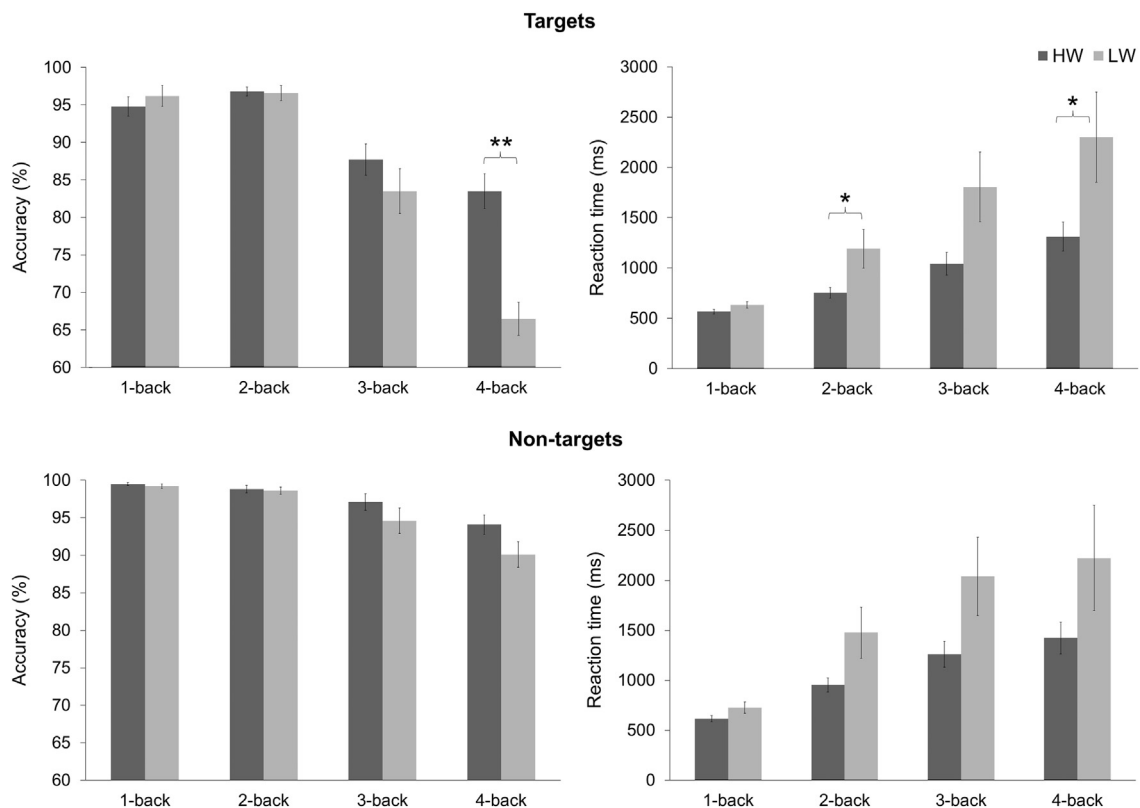
Fig. 2 – Behavioral results of the N-back task. **Mean accuracy (left) and reaction time (right) as a function of task load and group for targets (upper) and non-targets (lower).** $^{*}p < 0.05$; $^{**}p < 0.001$.

a different task, the Modified Digit Span (MODS) task (Daily et al., 2001; Lovett et al., 1999, 2000) prior to performing the N-back task. Performance on the MODS task was used to assign subjects into the high and low WM capacity (HW/LW) groups. In that way we could ask whether an independent estimate of WM capacity predicts behavioral and neural measures on the N-back task. With this method, any differences we observed between the groups could not be attributed to how individuals were affected by the N-back task, per se, but would be due to differences in WM capacity. Previous studies by Lovett and colleagues (Lovett et al., 1999, 2000) have shown that the MODS task can provide a reliable estimate of WM, and they

have also reported good fits for individual performance on other WM tasks such as serial recall and the N-back task by using the WM estimate derived from the MODS task.

2. Results

2.1. Behavioral results of the MODS task

Fig. 1, panel A plots the proportion of memory sets that were recalled without any errors as a function of the memory set size in the MODS task (see Daily et al., 2001; Lovett et al., 1999;

for a description of the task and the methods for estimating WM capacity). Lovett et al. (1999) developed a method to estimate W, an index of an individual's WM capacity based on the MODS task performance. W is assumed to have a mean of 1.0 and the range of values in our sample was from 0.6 to 1.5. Based on this distribution, subjects were split into a HW group and a LW group. The mean W for HW and LW groups are displayed in panel B of Fig. 1. A two-sample t-test yielded significant differences on W between the two groups ($t(26)=6.177$, $p<0.001$). Although the subjects were divided based on a median split of W, the average W scores were reliably different in the two groups.

2.2. Behavioral results of the N-back task

Mean accuracy and mean correct response times (RTs) in each memory load condition (1-, 2-, 3- and 4-back) for target and non-target stimuli for both WM groups are displayed in Fig. 2. A repeated-measures analysis of variance (ANOVA) was conducted on accuracy using memory load and stimulus type as within-subject factors, and group as a between-subject factor. Accuracy dropped with increasing memory load ($F(3, 78)=81.272$, $p<0.001$), and was lower for target than non-target stimuli ($F(1, 26)=108.675$, $p<0.001$). Performance was also worse for LW subjects than HW subjects ($F(1, 26)=7.02$, $p=0.01$). There was a significant interaction between load and stimulus (target vs. non-target) ($F(3,$ 78)$=46.956$, $p<0.001$) such that performance dropped more for targets than non-targets. Likewise there was an interaction of stimulus type and group ($F(1, 26)=4.347$, $p<0.05$) such that the accuracy difference between HW and LW groups was greater for targets than non-targets.

We also analyzed the accuracy data separately for each stimulus type. For non-target stimuli, there was only a significant effect of load condition ($F(3, 78)=30.044$, $p<0.001$). In contrast, for the target stimuli accuracy differed reliably between groups ($F(1, 26)=7.643$, $p=0.01$) as well as across load conditions ($F(3, 78)=82.937$, $p<0.001$). The effect of N-back load on accuracy was larger in the LW group, supported by an interaction of load and group ($F(3, 78)=14.102$, $p<0.001$). Post hoc analyses indicated that the HW group's advantage in accuracy over the LW group was only reliable in the 4-back condition ($t(26)=5.351$, $p<0.001$).

The same type of analysis used for accuracy was performed on the RT data. For target stimuli, RT increased with increasing memory load ($F(3, 78)=25.308$, $p<0.001$), and subjects in the HW group responded faster than those in the LW group ($F(1, 26)=4.806$, $p<0.05$). There was also a significant interaction of load and group ($F(3, 78)=3.704$, $p<0.05$). Post hoc analyses indicated that the HW group responded faster in the 2- ($t(26)=-2.198$, $p<0.05$) and 4-back ($t(26)=-2.096$, $p<0.05$) conditions. Like with accuracy measures, the only significant main effect for non-target stimuli was the manipulation of load ($F(3, 78)=19.645$, $p<0.001$).
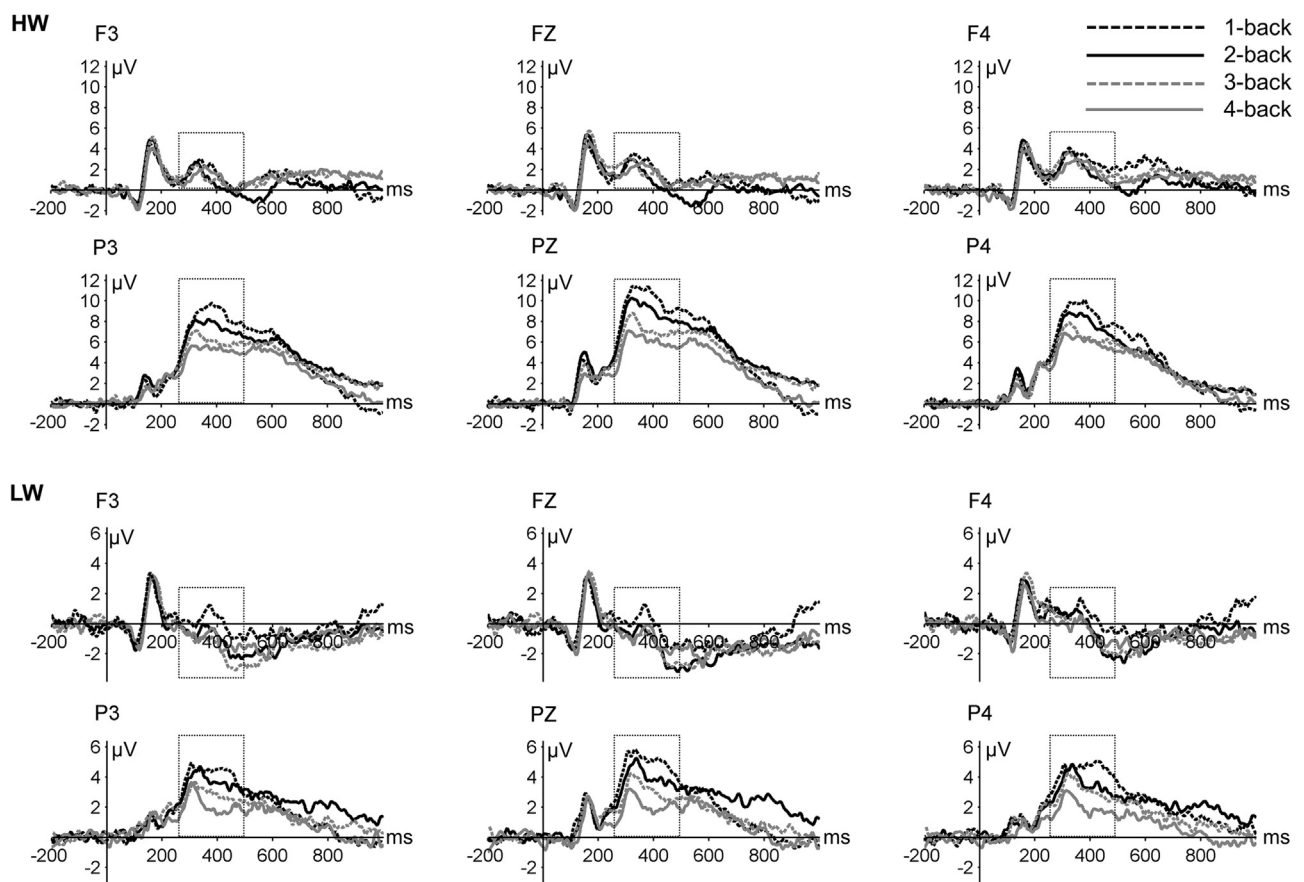

Fig. 3 – Grand-average ERP waveforms of the N-back task. **Grand-average ERPs as a function of task load at the frontal (F3, FZ, F4) and parietal (P3, PZ, P4) sites for HW (upper) and LW (lower) groups. Dashed squares on each graph represent the time windows used for analyses of the P300 component. Note that the scales of the y-axis are different for the two groups.**

Since group differences is of central importance to this study and we only observed reliable differences between the two groups for target stimuli (on either behavioral measure), we focus on the target stimuli for electrophysiological analyses presented below.

2.3.   ERP results

Grand-mean waveforms for the N-back task are shown for each memory load condition at the frontal and parietal sites for each group in Fig. 3. The P300 peak amplitude and latency data from the two regions are presented in Fig. 4. A repeated-measures ANOVA using memory load and electrode site as within-subject factors and group as a between-subject factor was applied to the P300 peak amplitude data. The amplitude of the P300 diminished as memory load increased ($F(3, 78) = 7.117$, $p < 0.001$) and the amplitude was larger at the parietal site than the frontal site ($F(1, 26) = 42.881$, $p < 0.001$). In addition, the effect of load interacted with site ($F(3, 78) = 3.261$, $p < 0.05$) such that the effect of load was larger at the parietal site. While the amplitude of the P300 was reliably greater for the HW group ($F(1, 26) = 10.181$, $p < 0.005$), no other factor interacted with the group variable, suggesting that the two groups showed the same trend across different load conditions and electrode sites. A parallel analysis was conducted for the P300 peak latency, and the only effect to reach significance was electrode site ($F(1, 26) = 4.796$, $p < 0.05$).

## 2.4.   ERS/ERD results

Given that the behavioral data showed the LW group was more affected by manipulations of WM load than the HW group but P300 waveforms did not display such a difference, we decided to investigate whether we would obtain a more sensitive measure

of our manipulations by examining ERS/ERD patterns. The electrodes selected for ERS/ERD analyses were those where we observed the biggest effects. Specifically, those showing task-related increases in theta-band power compared to the baseline period over frontal regions (spatial peaks around F3, FZ and F4, Fig. 5A) and those with the most pronounced task-related decreases in alpha-band power over parietal areas (spatial peaks around P3, PZ and P4, Fig. 5A) were selected.

Theta (~3–7 Hz) ERS responses: Grand-average time–frequency plots over the frontal region showed long-lasting (0–1750 ms) theta ERS responses (Fig. 5B). Condition-specific theta ERS data within the time–frequency window that produced the largest magnitudes (marked with a dashed square in Fig. 5B) are shown for each group in Fig. 6A. The repeated-measures ANOVA indicated that theta ERS responses declined reliably as the task became more difficult ($F(3, 78) = 18.873$, $p < 0.001$). While the magnitude of theta ERS was significantly greater for the HW group than the LW group ($F(1, 26) = 4.716$, $p < 0.05$), the difference in magnitude between groups did not change as a function of load (i.e., there was no interaction). Post hoc analyses indicated that the HW group exhibited larger theta ERS in the 1- ($t(26) = 2.185$, $p < 0.05$) and 4-back ($t(26) = 2.843$, $p < 0.01$) conditions relative to the LW group.

Alpha (~8–12 Hz) ERD responses: With regard to alpha-band, ERD responses were elicited at about 200 ms after stimulus presentation, as shown in the grand-average time–frequency plots over the parietal area (Fig. 5C). Condition-specific alpha ERD data within the time–frequency window that produced the largest ERD magnitudes (marked with a dashed square in Fig. 5C) are illustrated for each group in Fig. 6B. Contrast to theta ERS, alpha ERD responses did not vary significantly in magnitudes across the four load conditions even though group differences were still significant
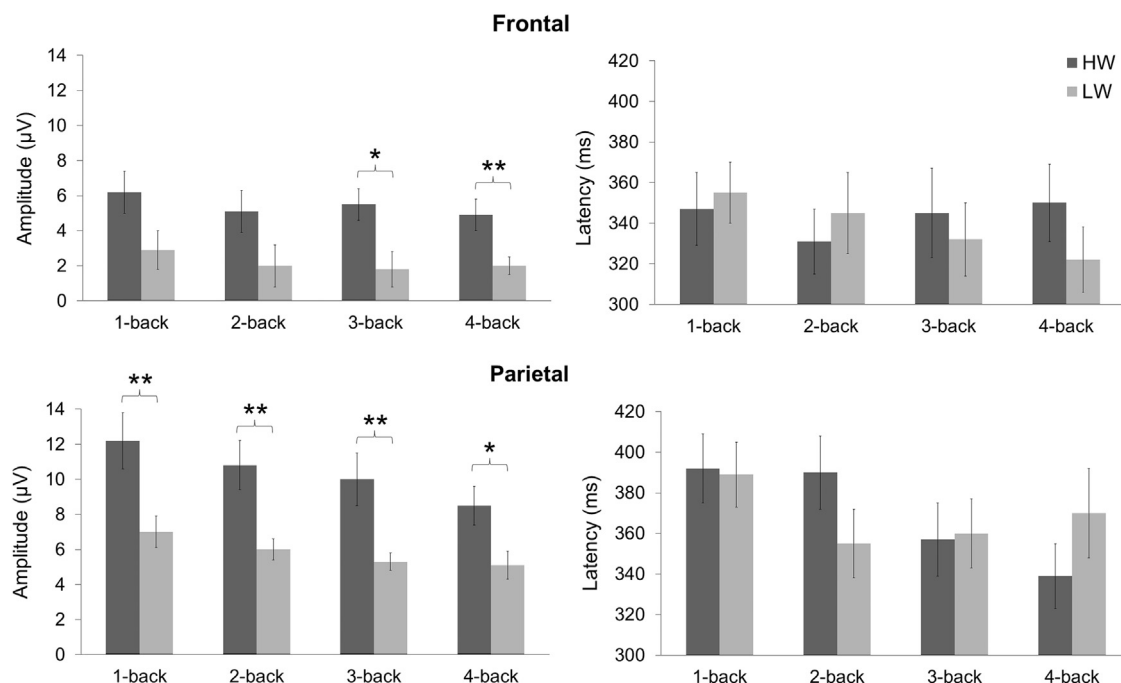
Fig. 4 – ERP results of the N-back task. Mean P300 peak amplitude (left) and latency (right) as a function of task load and group at the frontal (averaged across F3, FZ and F4, upper panel) and parietal (averaged across P3, PZ and P4, lower panel) sites. * $p < 0.05$; ** $p < 0.01$.
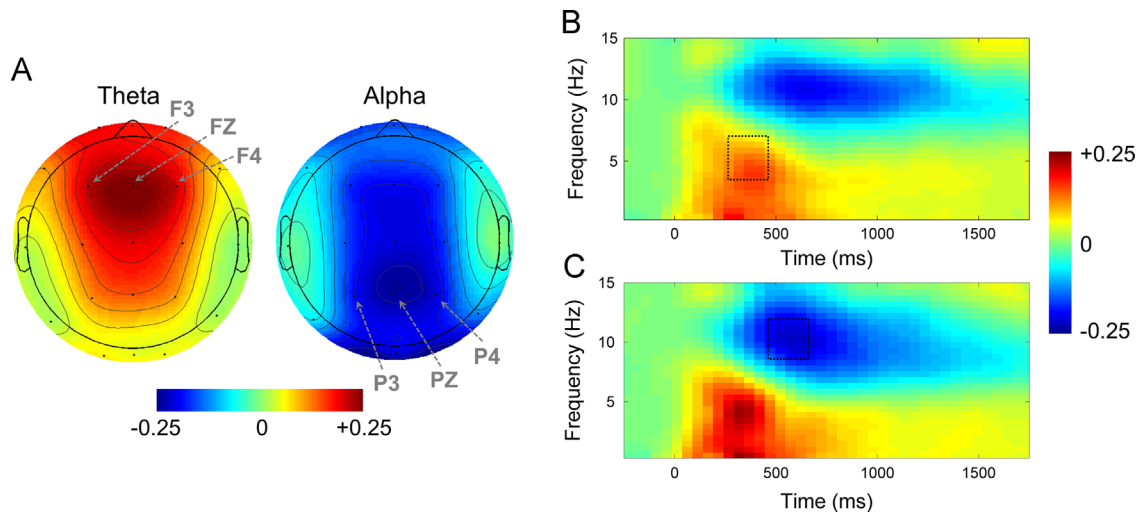
Fig. 5 – Task-related changes in theta and alpha power. **(A) Topographical maps of theta ERS and alpha ERD averaged over 100–700 ms post-stimulus; (B) Grand-average time–frequency ERS/ERD plots over frontal electrodes (averaged F3, FZ and F4); (C) Grand-average time–frequency ERS/ERD plots over parietal electrodes (averaged P3, PZ and P4). Dashed squares in (B) and (C) represent the time–frequency windows used for statistical analyses.**

$(F(1, 26)=5.042, p<0.05)$. Post hoc analyses showed that the HW group exhibited reliably lower magnitudes of alpha ERD in the 1- $(t(26)=-2.102, p<0.05)$, 3- $(t(26)=-2.164, p<0.05)$, and 4-back $(t(26)=-2.303, p<0.05)$ conditions compared with the LW group.

2.5. Comparison of different measures

Pearson correlation coefficients were computed for each load condition between W values and all the behavioral and electrophysiological variables, including the N-back task accuracy and RT, ERP and ERS/ERD measures. As is shown in Table 1, more variables tended to correlate with the W values as the memory load increased. For instance, in the 1-back condition, only the P300 amplitude and alpha ERD at the parietal site were associated with W; while in the 4-back condition, all the variables except for the RT and parietal P300 latency were closely related to W. Nevertheless, the parietal P300 amplitude and alpha ERD correlated with W regardless of WM demands. That is, subjects with higher W values produced greater P300 amplitudes as well as lower alpha ERD responses at all difficulty levels of the WM task.

In order to further compare the three sets of analyses in the current study, the statistical power (η_p^2) for each measurement was computed to compare effect sizes of WM-based group differences across behavioral, ERP and EEG measures (Gulbinaite et al., 2014). These are summarized in Fig. 7. As can be seen from the figure, the behavioral measures have similar effect sizes compared with EEG measures, while one of the ERP measures, P300 amplitude over the parietal region, produced the largest effect size. This suggests that the index of P300 amplitude is a more sensitive measure of WM-related differences than others.

3. Discussion

Previous research has examined changes in electrophysiological response as a function of WM demands (Daffner et al., 2011;

Jaeggi et al., 2007; McEvoy et al., 2001; Pesonen et al., 2007; Watter et al., 2001), but less research has focused on whether these changes vary across individuals with different WM capacities. The current study aimed to uncover whether there are electrophysiological signatures that distinguish individuals with high vs. low WM capacities, and to see whether such electrophysiological differences are only manifest when WM is severely challenged or the differences are apparent even in relatively easy WM tasks. While previous studies that have explored individual differences in WM tasks have used performance on the task itself as a way to distinguish among subjects (e.g., Daffner et al., 2011; Jaeggi et al., 2007), we opted to use an unrelated WM task to classify subjects prior to asking them to perform in the N-back task. By using the MODS task (Daily et al., 2001; Lovett et al., 1999, 2000) to derive an independent estimate of WM capacity, any differences we observed in the N-back task between groups could not be due exclusively to how people performed in the N-back task itself.

Consistent with previous studies that categorized subjects' WM capacities based on performance on the N-back task (Daffner et al., 2011; Jaeggi et al., 2007), we found that our independently classified HW and LW subjects also showed load-dependent changes in the P300, theta ERS and alpha ERD patterns for both groups, with differences between groups larger at the most challenging level of the N-back. An important distinction between our study and previous ones is that previous researchers speculated that differences in the observed neural activity patterns between groups were due to differences in strategy or an exhaustion of WM capacity (e.g., Jaeggi et al., 2007; Vogel et al., 2005). Our results, however, showed similar differences in the neural patterns between groups even at the lowest level of N-back difficulty, suggesting that more is going on than merely differential adoption of strategies at the highest level of N-back or complete depletion of WM resources. Specifically, in the 1-back task, both HW and LW subjects performed near ceiling, indicating that the task was not challenging and did not tax WM. Given that our subjects were classified based on their
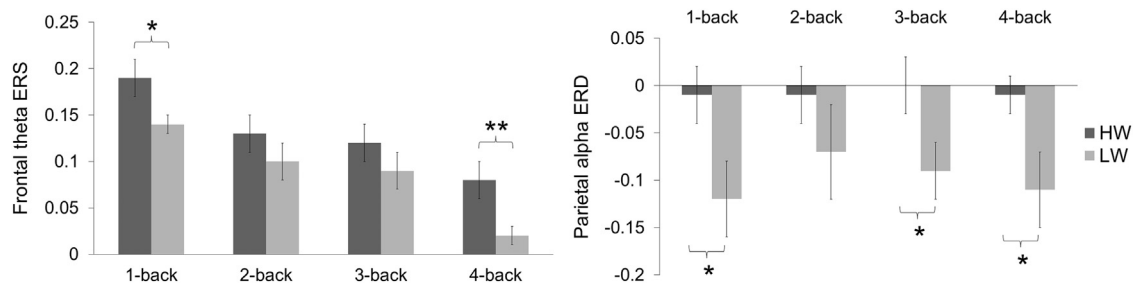
Fig. 6 – EEG results of the N-back task. **The left graph represents theta ERS responses as a function of task load and group at the frontal site (averaged F3, FZ and F4); the right graph represents alpha ERD responses as a function of task load and group at the parietal site (averaged P3, PZ and P4).** * $p < 0.05$; ** $p < 0.01$.

Table 1 – Pearson correlation coefficients computed between W (estimates of individual's working memory capacity) values and the behavioral and electrophysiological measures for each memory load condition ($n = 28$)[a]

	W			
	1-Back	2-Back	3-Back	4-Back
Accuracy	−0.21	0.17	0.25	0.83**
RT	−0.20	−0.34*	−0.31	−0.31
F_P300 amplitude	0.30	0.28	0.46**	0.50**
F_P300 latency	0.15	0.24	0.34*	0.45*
P_P300 amplitude	0.38*	0.49**	0.46**	0.43*
P_P300 latency	−0.08	0.18	−0.08	−0.03
F_theta ERS	0.32	0.10	0.12	0.57**
P_alpha ERD	−0.34*	−0.39*	−0.39*	−0.45*

[a] F, frontal; P, parietal. F_theta ERS here denotes the value of theta ERS at the frontal site during 250–450 ms; P_alpha ERD represents the absolute value of alpha band ERD at the parietal site during 450–650 ms.
* $p < 0.05$.
** $p < 0.01$.
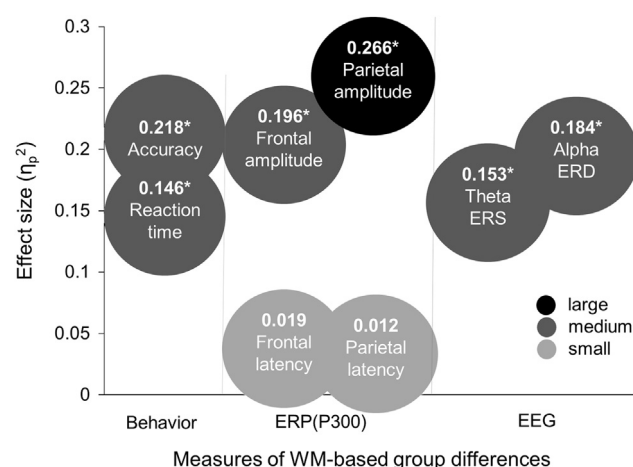
Fig. 7 – Summary of results depicting effect sizes of different measures. **The color of the circles represents small (light gray), medium (dark gray) and large (black) effect sizes in the current study. Asterisks denote analyses in which the effect of WM was significant.**

behavioral performance in a different task, it seems unlikely that the difference could be due to strategy adoption, per se. As further evidence that these observed neural differences between groups are not based solely on task difficulty, we found that both the P300 amplitudes and alpha ERD magnitudes correlated with WM capacities (estimated from the independent task we used to classify subjects), and those correlations did not factor in task difficulty. Taken together, our findings suggest that qualitative neural differences exist among individuals with different WM capacities. Below we provide further evidence for this position.

3.1. The effects of excessively challenging tasks on LW subjects

Very few studies have examined the neural markers of excessive demands on WM. The fMRI study by Jaeggi et al. (2007) investigated the cortical activation patterns when individuals' WM capacity limits were reached or even exceeded. Their subjects tried to perform two N-back tasks concurrently, one auditory and one spatial. They found that those subjects who performed poorly in the 3-back dual-task showed significantly greater activation in prefrontal areas than the high performing group. They speculated that the low performing group used less effective strategies than the high performers. In the current study, we examined the electrophysiological signatures of individual differences in WM capacities under the excessively demanding 4-back task and found large differences between HW and LW groups as well. Like Jaeggi et al. (2007)'s results of greater activation for poorer performers, we found that our LW subjects showed enhanced alpha ERD, the magnitudes of which are proportional to the amount of cortical neurons recruited into a transient functional network for task performance (Gevins and Smith, 2000; Klimesch, 1999). This suggests that LW individuals need to integrate relatively more neural resources to accomplish a demanding cognitive task and may recruit additional resources irrelevant or even detrimental to the current performance.

We also observed smaller P300 amplitudes and theta ERS for the LW subjects in the challenging 4-back task. The P300 amplitude has been thought to reflect the limits on cognitive resources that can be allocated to concurrent operations such that the smaller the P300 the less available WM resources (McEvoy et al., 1998; Watter et al., 2001). The smaller P300 amplitudes observed in the LW group thus suggest that individuals with lower WM capacities have fewer cognitive resources to allocate to the demanding task and are more influenced by other competing operations or thoughts. Theta

ERS is also thought to index the extent of cognitive resources. For example, when sustained mental effort is required, theta ERS is frequently observed (Gevins et al., 1997) and it is thought to be associated with the functioning of the central executive aspect of WM (Sauseng et al., 2005). Norman et al. (2007) proposed that theta oscillations can also function to facilitate memory retrieval and suppress competing memories. Based on our findings and the prior research, it seems plausible to conclude that during demanding cognitive tasks, individuals with LW capacities are less able to exert additional effort to control the functioning of the central executive and avoid interference from irrelevant information, consistent with our interpretation of the ERP results.

3.2.   Qualitative differences or strategy differences?

The above findings suggest that individuals with different WM capacities differ in their ability to allocate attention as well as in their efficiency to use neural resources to perform challenging cognitive tasks. One might wonder whether the effects we observed under the most demanding condition resulted from subjects' differential tendency to give up on the task, or adopt a different strategy when the task is especially challenging (e.g., Jaeggi et al., 2007). To explore this possibility, we compared the neural differences between the two groups at the lowest difficulty level, when both groups could easily perform the task. Interestingly, the same group differences in the pattern of P300, theta ERS and alpha ERD responses were manifest in the 1-back task compared with the 4-back. That finding makes an explanation based on strategy differences, per se, or differential "quitting" on hard tasks less tenable. It is also unlikely that the observed differences in the 4-back condition were somehow an artifact of a floor effect for the LW group. While the LW subjects certainly found the 4-back task more challenging than did the HW subjects, their performance was still reliably above chance even for the targets. Given that group differences in the neural responses (particularly, the P300 amplitudes and alpha ERD patterns) were consistent across all levels of difficulty, it is difficult to argue that the difference in neural patterns for the two groups is based on a strategy difference or performance difference. In addition, the two WM groups were assigned based on performance of an independent task, and thus our a priori determination of WM capacity allows us to account for differences in the electrophysiological patterns without postulating strategic or other differences.

A particularly compelling result related to neural correlates of individual differences came from the finding that both the P300 amplitudes and alpha ERD magnitudes were found to correlate with WM capacities independent of the task difficulty. Taken together, these findings suggest that there are qualitative differences among individuals with different WM capacities when engaging in cognitive operations. Specifically, individuals with higher WM capacities (compared to those with lower WM) can make more efficient use of neural resources to support functioning of the central executive.

3.3.   Summary

In summary, the current study used a separate task to define WM capacity prior to the N-back task. We found that task performance of LW subjects was more affected by increasingly WM demands. In terms of the electrophysiological measures, there were large inter-individual differences in both ERP and EEG oscillatory patterns during cognitive processing at excessive WM demands, and such differences were also observed to exist even when individuals performed near ceiling. Furthermore, the P300 amplitudes and alpha ERD magnitudes were observed to correlate with WM capacities independent of task difficulty. The P300 amplitudes, in particular, were found to better capture the WM-related differences among individuals. Therefore, our independent estimate of WM capacity was supported both by the behavioral performance and the neural evidence. Our results suggest that there are qualitative neural differences among individuals with different WM capacities when approaching cognitive operations. Specifically, individuals with higher WM capacities can make efficient use of their neural resources to keep focused attention on the task-relevant information. Given the centrality of WM to human cognitive processing, this study would help us to further understand the neural mechanisms associated with individual differences in WM capacity. To the best of our knowledge, there are few studies on electrophysiological responses at mental overload, and thus our findings may also provide fresh insights into this area.
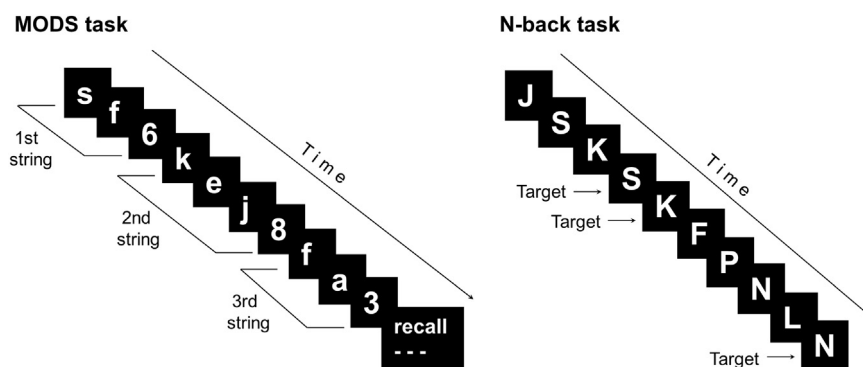
4.   Experimental procedures

4.1.   Subjects

A total of 28 undergraduate students (16 males, mean ages of 19.7 years) from Carnegie Mellon University participated in this study. All subjects were right-handed young adults with normal or corrected-to-normal vision. For their participation, subjects were given credit towards fulfillment of a research experience requirement.

4.2.   Experimental design and procedure

Subjects first participated in the MODS task (Daily et al., 2001; Lovett et al., 1999, 2000) in order to get an independent estimate of WM capacity. Panel A of Fig. 8 provides an illustration of a trial from this task. The subject's task was to recall, in chronological order, the final digit of each "string" presented on that trial. The number of strings varied across trials as did the number of letters presented in a string before the digit that terminated each string. Subjects were required to read each character aloud as it appeared, at a rate of 910 ms per character, and maintain the string-final digits in memory. At the end of each trial, a recall prompt appeared and subjects were told to enter the digits from that trial in the exact order as they were presented. The more digits that needed to be recalled, the greater the memory set size, from 3 to 6. Subjects' performance was then evaluated according to their accuracy in the recall.

Immediately after performing the MODS task, subjects were asked to participate in the N-back task, with scalp EEG signal recorded simultaneously. Panel B of Fig. 8 illustrates the procedure for the N-back task in the 2-back condition. The values of N in the N-back task varied from 1 to 4. For convenience, we will refer to these different values of N in the N-back task as differences in WM load, with the larger values

Fig. 8 – Procedures of the experimental tasks. **(A) The procedure of one trial in the MODS task; (B) The procedure of the N-back task in the 2-back condition.**

of N assumed to be conditions of higher WM load. For each load condition, there were six blocks, and the order of blocks was randomly determined for each subject. For a given block, 18 to 22 stimuli would be displayed, with 5 to 7 target stimuli per block. Overall, there were 36 target and 84 non-target stimuli for each load. A set of letters were presented one at a time and subjects were instructed to compare the currently displayed letter with the one presented N trials earlier. A letter was a target when it matched the stimulus shown N items previously (in the illustration of Fig. 8, N=2); all other letters were treated as non-targets. The stimulus stayed on the screen until the subject responded and then disappeared and the next stimulus appeared 2.5 s later. By allowing the task to be self-paced (see Krause et al., 2000; Pesonen et al., 2007), the highest load conditions (3- and 4-back) may not have been impossible. At the same time, allowing subjects to go as quickly as desired for easier trials minimized the risk of boredom. Assignment of target and non-target keys to left or right hand was counter-balanced. Subjects were given 20 practice trials for each load condition before performing the task formally and feedback was provided after each response only during the practice trials.

4.3. EEG recording

Subjects were tested in an electrically shielded and dimly lit room during EEG recording. EEG activity was recorded continuously with SynAmps amplifiers from 21 Ag–AgCl sintered electrodes (FP1, FPZ, FP2, F7, F3, FZ, F4, F8, T7, C3, CZ, C4, T8, P7, P3, PZ, P4, P8, O1, OZ, O2) using a 64-channel Quick-cap (10–20 system) of a NeuroScan system. The vertical EOG was recorded from two electrodes placed above and below the left eye, and the horizontal EOG was recorded from two electrodes placed at the external canthi of both eyes. Scalp recordings were referenced on-line to the left mastoid, and were further re-referenced off-line to the average of the two mastoids. All signals were digitized at a sampling rate of 1000 Hz, and were filtered with a band-pass of 0.01–100 Hz. Electrode impedances were kept below 5 kΩ.

4.4. Behavioral analyses

Performance on the MODS task was assessed according to the criterion that all of the digits in the memory set (a trial) had to

be recalled in their correct serial positions. An individual's mean performance for given levels of set size was then used to estimate W, a measure of an individual's WM capacity (see Daily et al., 2001; Lovett et al., 1999; etc.). Subjects were median split by W into a HW group and a LW group, with 14 subjects in each group.

With respect to the N-back task, mean accuracy and mean RT for correct trials were analyzed in each memory load condition for target and non-target stimuli for each group. The statistical significance of the differences in the measures across task conditions and between the two groups was analyzed using repeated-measures ANOVA.

4.5. ERP analyses

ERP analyses were conducted only for correct responses to the target stimuli. Vertical and horizontal ocular artifacts were corrected using an independent component analysis (ICA) based algorithm (Delorme and Makeig, 2004). After the correction, the continuous EEG data were segmented into epochs from −200 to 1000 ms locked to stimulus onset. Data were then baseline-corrected with respect to the pre-stimulus interval and low-pass filtered at 50 Hz. Epochs exceeding $\pm 100\,\mu V$ were rejected as artifacts. The average number of observations per condition per group included in the statistical analysis were as follows: for the HW group, there were 34 (SD=2), 35 (SD=1), 31 (SD=3) and 30 (SD=3) for 1-, 2-, 3- and 4-back, respectively; for the LW group, there were 35 (SD=2), 35 (SD=1), 31 (SD=3) and 24 (SD=3) for 1-, 2-, 3- and 4-back conditions. Peak amplitude and latency of the P300 component were measured with a time window of 250–500 ms after the onset of stimuli at frontal (F3, FZ and F4) and parietal (P3, PZ and P4) electrodes.

4.6. ERS/ERD analyses

The preprocessing procedures were the same as for the ERP analyses, except that the continuous EEG data were segmented into epochs from −500 to 2000 ms around stimulus onset. Each epoch was split into overlapping data segments of 500 ms, and the overlap was 450 ms. Within each individual segment, the Hann window function (defined as $\omega(n) = 0.5(1 - \cos(2\pi n/(N-1)))$, where N represents the window width and $0 \leq n \leq N-1$) was applied, and the time–frequency decomposition was performed

using the discrete Fourier transform (DFT) (defined as $X(f) = \sum_{n=0}^{N-1} x_n e^{-i2\pi f n}$, where f represents the frequency). The mean squared magnitude of the DFT results was regarded as the power at the center of each segment. The power data were then averaged across epochs to produce absolute power values as a function of time and frequency for each subject in each load condition. The average power during the time window prior to each stimulus presentation was calculated as the power over the reference period. The percentage of relative difference in the power of EEG between the stimulus presentation and the reference was expressed as ERS/ERD, in which positive values reflect relative power increase (ERS) and negative values reflect relative power decrease (ERD) (Krause et al., 2000; Pfurtscheller and Aranibar, 1977; Pfurtscheller and Lopes da Silva, 1999; Sauseng et al., 2005). In order to draw the regions of interest for theta and alpha band, topographical plots for task-related power changes in the two frequency bands within 100–700 ms were created respectively and averaged over all conditions and subjects (Fig. 5A). Electrodes that showed the largest ERS/ERD magnitudes were selected, and grand-average time–frequency ERS/ERD plots were constructed for these electrodes. Time–frequency windows with the largest magnitudes were selected based on visual inspection (marked with dashed squares in Fig. 5B and C). The condition-specific ERS/ERD data within these windows were extracted for each subject for statistical analyses.

Acknowledgments

REFERENCES

Alloway, T.P., 2009. Working memory, but not IQ, predicts subsequent learning in children with learning difficulties. Eur. J. Psychol. Assess. 25, 92.

Alloway, T.P., Alloway, R.G., 2010. Investigating the predictive roles of working memory and IQ in academic attainment. J. Exp. Child Psychol. 106, 20–29.

Baddeley, A., 1992. Working memory. Science 255, 556–559.

Baddeley, A., 2003. Working memory: looking back and looking forward. Nat. Rev. Neurosci. 4, 829–839.

Bastiaansen, M., Hagoort, P., 2003. Event-induced theta responses as a window on the dynamics of memory. Cortex 39, 967–992.

Braver, T.S., et al., 1997. A parametric study of prefrontal cortex involvement in human working memory. NeuroImage 5, 49–62.

Conway, A.R., 1996. Individual differences in working memory capacity: more evidence for a general capacity theory. Memory 4, 577–590.

Conway, A.R., et al., 2002. A latent variable analysis of working memory capacity, short-term memory capacity, processing speed, and general fluid intelligence. Intelligence 30, 163–183.

Daffner, K.R., et al., 2011. Mechanisms underlying age-and performance-related differences in working memory. J. Cogn. Neurosci. 23, 1298–1314.

Daily, L.Z., Lovett, M.C., Reder, L.M., 2001. Modeling individual differences in working memory performance: a source activation account. Cogn. Sci. 25, 315–353.

Daneman, M., Carpenter, P.A., 1980. Individual differences in working memory and reading. J. Verbal Learn. Verbal behav. 19, 450–466.

Delorme, A., Makeig, S., 2004. EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. J. Neurosci. Methods 134, 9–21.

Dempster, F.N., Cooney, J.B., 1982. Individual differences in digit span, susceptibility to proactive interference, and aptitude/achievement test scores. Intelligence 6, 399–416.

Engle, R., 1994. Individual differences in memory and their implications for learning. Encycl. Intell., 700–704.

Engle, R.W., et al., 1999. Working memory, short-term memory, and general fluid intelligence: a latent-variable approach. J. Exp. Psychol.: Gen. 128, 309.

Gevins, A., et al., 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.

Gevins, A., Smith, M.E., 2000. Neurophysiological measures of working memory and individual differences in cognitive ability and cognitive style. Cereb. Cortex 10, 829–839.

Grabner, R., et al., 2004. Intelligence and working memory systems: evidence of neural efficiency in alpha band ERD. Cogn. Brain Res. 20, 212–225.

Gulbinaite, R., van Rijn, H., Cohen, M.X., 2014. Fronto-parietal network oscillations reveal relationship between working memory capacity and cognitive control. Front. Hum. Neurosci., 8.

Jaeggi, S.M., et al., 2007. On how high performers keep cool brains in situations of cognitive overload. Cogn. Affect. Behav. Neurosci. 7, 75–89.

Jaeggi, S.M., et al., 2010. The relationship between n-back performance and matrix reasoning—implications for training and transfer. Intelligence 38, 625–635.

Juvina, I., Taatgen, N.A., 2007. Modeling control strategies in the n-back task. In: Proceedings of the Eighth International Conference on Cognitive Modeling. 73–78.

Klimesch, W., 1999. EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis. Brain Res. Rev. 29, 169–195.

Krause, C.M., et al., 2000. The effects of memory load on event-related EEG desynchronization and synchronization. Clin. Neurophysiol. 111, 2071–2078.

Lee, H., et al., 2005. Phase locking of single neuron activity to theta oscillations during working memory in monkey extrastriate visual cortex. Neuron 45, 147–156.

Lovett, M.C., Reder, L.M., Lebiere, C., 1999. Modeling working memory in a unified architecture. Models of Working Memory: Mechanisms of Active Maintenance and Executive Control. 135-182.

Lovett, M.C., Daily, L.Z., Reder, L.M., 2000. A source activation theory of working memory: cross-task prediction of performance in ACT-R. Cogn. Syst. Res. 1, 99–118.

Manelis, A., Reder, L.M., 2014. Effective connectivity among the working memory regions during preparation for and during performance of the n-back task. Front. Hum. Neurosci., 8.

McEvoy, L.K., Smith, M.E., Gevins, A., 1998. Dynamic cortical networks of verbal and spatial working memory: effects of memory load and task practice. Cereb. Cortex 8, 563–574.

McEvoy, L.K., et al., 2001. Neurophysiological signals of working memory in normal aging. Cogn. Brain Res. 11, 363–376.

Norman, K.A., Newman, E.L., Detre, G., 2007. A neural network model of retrieval-induced forgetting. Psychol. Rev. 114, 887.

Owen, A.M., et al., 2005. N-back working memory paradigm: a meta-analysis of normative functional neuroimaging studies. Hum. Brain Mapp. 25, 46–59.

Pesonen, M., Hämäläinen, H., Krause, C.M., 2007. Brain oscillatory 4–30 Hz responses during a visual n-back memory task with varying memory load. Brain Res. 1138, 171–177.

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.

Polich, J., 2007. Updating P300: an integrative theory of P3a and P3b. Clin. Neurophysiol. 118, 2128–2148.

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

Turner, M.L., Engle, R.W., 1989. Is working memory capacity task dependent?. J. Mem. Lang. 28, 127–154.

Verhaeghen, P., Basak, C., 2005. Ageing and switching of the focus of attention in working memory: results from a modified N-back task. Q. J. Exp. Psychol. Sect. A 58, 134–154.

Vogel, E.K., McCollough, A.W., Machizawa, M.G., 2005. Neural measures reveal individual differences in controlling access to working memory. Nature 438, 500–503.

Watter, S., Geffen, G.M., Geffen, L.B., 2001. The n-back as a dual-task: P300 morphology under divided attention. Psychophysiology 38, 998–1003.