bioRxiv preprint doi: https://doi.org/10.1101/098301; this version posted January 4, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

EEG correlates of working memory performance in females

Yuri G. Pavlov[1,2], Boris Kotchoubey[1]

[1] Institute of Medical Psychology and Behavioural Neurobiology, University of Tübingen, Tübingen, Germany

[2] Department of Psychology, Ural Federal University, Yekaterinburg, Russia

Yuri G. Pavlov pavlovug@gmail.com

Boris Kotchoubey boris.kotchoubey@uni-tuebingen.de

bioRxiv preprint doi: https://doi.org/10.1101/098301; this version posted January 4, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

Abstract

Background

The study investigates oscillatory brain activity during working memory (WM) tasks. The tasks employed varied in two dimensions. First, they differed in complexity from average to highly demanding. Second, we used two types of tasks, which required either only retention of stimulus set or retention and manipulation of the content. We expected to reveal EEG correlates of temporary storage and central executive components of WM and to assess their contribution to individual differences.

Results

Generally, as compared with the retention condition, manipulation of stimuli in WM was associated with distributed suppression of alpha1 activity and with the increase of the midline theta activity. Load and task dependent decrement of beta1 power was found during task performance. Beta2 power increased with the increasing WM load and did not significantly depend on the type of the task.

At the level of individual differences, we found that the high performance (HP) group was characterized by higher alpha rhythm power. The HP group demonstrated task-related increment of theta power in the left anterior area and a gradual increase of theta power at midline area. In contrast, the low performance (LP) group exhibited a drop of theta power in the most challenging condition. HP group was also characterized by stronger desynchronization of beta1 rhythm over the left posterior area in the manipulation condition. In this condition, beta2 power increased in the HP group over anterior areas, but in the LP group over posterior areas.

Conclusions

WM performance is accompanied by changes in EEG in a broad frequency range from theta to higher beta bands. The most pronounced differences in oscillatory activity between individuals with high and low WM performance can be observed in the most challenging WM task.

bioRxiv preprint doi: https://doi.org/10.1101/098301; this version posted January 4, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

Background

The ability to retain information in memory for a short period of time is critical for numerous cognitive tasks including planning, verbal competence, spatial orientation, mental manipulations of objects and many others [12–14].

According to Baddeley & Hitch's [15] model, the structure of working memory (WM) consists of several components. One of them is responsible for temporary storage of information in modality-specific buffers. Another key component, the central executive, is considered to be a set of tools designed to maintain the active representation of memory trace, to control attention and to preserve the latter from interference caused by irrelevant stimuli [16,17].

A number of neuroimaging studies demonstrated that maintenance of information in WM engages a broad network of neural structures mostly including prefrontal cortex, parietal and temporal areas [13,18]. Whereas storage buffers represent information received from sensory inputs in posterior regions, the prefrontal cortex sustains and transforms this information and organizes executive processes of working memory [19]. Existing research highlights the importance of the fronto-parietal network activation in working memory processes, especially in high demanding tasks [20–24]. Apparently, individual differences in working memory capacity are also determined by fronto-parietal white matter connectivity [25].

Features of the processes presumed by Baddeley & Hitch's model of WM cannot be characterized only by spatial distribution of brain activation. Qualitatively different information about these processes can be obtained from studies of neuronal oscillatory activity as an energy-efficient mechanism for temporal coordination of cognitive processes [26].

An increase of frontal midline *theta* rhythm (FMT) frequently accompanies such processes as nonspecific attention and WM [3,27–29]. The results of earlier studies often define FMT as the most plausible phenomenon reflecting an activation of central executive components of WM [30]. Several attempts to isolate central executive components from temporary storage components by including tasks requiring mental manipulations support hypothesis of the link between FMT and the executive control [31–33]. Several studies demonstrated the activation of fronto-parietal executive control system during retention

bioRxiv preprint doi: https://doi.org/10.1101/098301; this version posted January 4, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

in WM [34–36]. Moreover, some authors report increasing fronto-parietal synchronization with stronger engagement of central executive components [29]. Induced coupling of theta rhythm between frontal and parietal cortical regions by transcranial alternating current stimulation (tACS) resulted in improved visual WM performance, while the induced decoupling lead to WM deterioration [37].

Changes in *alpha* activity also show parametrical increase related to working memory load [38–40]. Increasing power of alpha rhythm is frequently interpreted as a mechanism for filtration and for suppression of the cortical areas irrelevant to the current task [40–42].

The role of *beta* activity in working memory processes is still not sufficiently investigated. Thus the activity particularly in the low beta band (~13-20 Hz) was found to increase during retention in WM [3,43–45]. A parametrical increase of low beta with the increasing of memory set size was also observed [3,43]. A comparison of retention condition with the conditions where participants were instructed to manipulate objects in WM showed that gradually increasing task complexity was related with a decrease of low beta activity [32].

Data of several studies suggest that the main contribution to individual differences in WM is made by the ability to control attention or executive control [46–48]. However, despite extensive research of WM in the recent 20 years, there is no clarity as regards the electrophysiological correlates mechanisms of individual differences in WM performance. The existing research (both general and differential psychological) have some limitations that restrict the possibility to explain the actual relationship between brain activity and WM performance.

First of all, most WM studies have used the n-back paradigm [1,2,49]. This kind of task engages multiple WM processes including retention of the stimuli set presented at the previous step, comparison between the first item of the memorized set and the new one, making decision about correctness of the comparison, and updating the content of WM. In this paradigm, it is difficult to clearly separate retention from the central executive components of WM.

Second, the level of difficulty of the task is usually moderate and thus does not present a big challenge for people with average WM abilities. There are studies dedicated to the investigation of EEG in

bioRxiv preprint doi: https://doi.org/10.1101/098301; this version posted January 4, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

WM tasks with several levels of difficulty [1,3,4,9]. In the studies mentioned above the number of steps did not exceed three (3-back) [1,2]. Some researchers applied other paradigms with gradually increasing difficulty of tasks for assessing WM performance [3,28,33]. But these paradigms either did not include any manipulation task [3,28], or their difficulty level was rather low [33].

Finally, the existing studies aimed to discover electrophysiological correlates of individual differences in WM were based on a sample size not exceeding 14 participants in each group [1,3,50]. An analysis of typical effect sizes indicates that at least twice larger groups would be necessary to reliably evaluate the differences between high- and low-performers.

In this paper we used highly demanding tasks which should give us the opportunity to distinguish EEG activity of individuals with different levels of WM performance. Additionally, using two types of tasks, which required either only retention of stimulus set or manipulation of content, we expected to reveal EEG correlates of temporary storage and central executive components of WM and to assess their contribution to individual differences.

The hypotheses of the study were as follows:

1. Motivated by the previous studies we expected significant relationships between WM performance and oscillatory activity in theta and alpha frequency bands;

2. Particularly, we supposed that frontal theta rhythm power is strongly related to the WM load;

3. We expected that storage components of working memory play less important role in individual differences than executive components. Specifically, we assumed that no individual differences would be found in the simple retention conditions;

4. Additionally, we hypothesized that the most challenging condition would best separate between low and high performers;

Methods

Participants

bioRxiv preprint doi: https://doi.org/10.1101/098301; this version posted January 4, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

Due to a strong gender disproportion in the initial sample, only data of female participants were included into the present study. All participants were Russian native speakers. Furthermore, a subsequent analysis revealed five EEG records with an excessive amount of artefacts (i.e., less than 20 artifact-free epochs in at least one condition). Thus, 65 female participants (mean age = 20.92, SD=2.96) were included to the final sample. The participants had normal or corrected-to-normal vision and no history of neurological or mental diseases.

Stimuli

Sets of Russian alphabet letters written in capital were used as stimuli. The letters had been selected randomly and had random order and no repetitions in the sets. Each trial consisted of 7 consecutive events. An analogue using Latin letters and English words is shown in Fig. 1.

Insert Figure 1 about here

A trial always began with an exclamation mark presented for 200 ms, which was followed by a fixation cross for 3000 ms. Participants were instructed to fixate the cross when it appeared in the center of the screen. At the next step the word “forward” or “alphabetical”, presented for 500 ms, instructed participants whether they would have to memorize the original set as it was presented (retention task) or to memorize it after mental recombination of the letters in the alphabetical order (manipulation task). After that, sets of 5, 6 or 7 letters were demonstrated for 3000 ms followed by a delay period where a fixation cross was demonstrated for 6500 ms. At the end of this delay period, a randomly chosen letter from the previously presented set appeared on the screen together with a digit that represented the serial number of this letter. The letter-digit combination was presented for 1000 ms. Participants were asked to press a specified button of a computer mouse if the presented letter had the corresponding serial number either in

bioRxiv preprint doi: https://doi.org/10.1101/098301; this version posted January 4, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

the original set (in the retention task), or in the set merging as a result of alphabetic recombination (in the manipulation task). The other mouse button had to be pressed if the serial number of the presented letter was incorrect. The two buttons were attributed to correct and wrong probes in a counterbalanced order. The probe was correct in 50 % of the trials, and the order of correct and incorrect probes was random. The next trial started after an interval that varied between 5000 and 5500 ms.

Thus, the experiment entailed six different conditions: memorizing 5, 6 or 7 letters in the alphabetical or forward order. Each condition had 20 consecutive trials. These six blocks with 20 trials were presented in a random order. A short practice block of 6 trials was given immediately before the main experiment.

During the experiment, the participants were seated in a comfortable armchair in front of a com puter screen in a dark room. Stimuli were presented in white color on a black background in the center of the screen by using PsyTask software (Mitsar Ltd.). The distance to the screen was 1 m and the size of the letters was 1.2 × 1.2°.

All participants were subdivided into two groups separated by the median of their mean performance across all tasks. The groups are referred to as high performance (HP; N = 32) and low performance (LP; N = 33) groups. The percentage of correct answers was used for behavioral data analysis. A repeated measures ANOVA with the between-subject factor Group (HP, LP) and the within-subject factors Task (retention, manipulation) and Load (5, 6, or 7 letters) was applied.

EEG recording and analysis

The EEG was recorded from 19 electrodes arranged according to the 10-20 system using Mitsar-EEG-201 amplifier and referred to the average earlobe. Two additional electrodes were used for horizontal and vertical EOG. EEG data were acquired with 500 Hz sampling frequency, 0.16 Hz high pass filter and 70 Hz low pass filter.

bioRxiv preprint doi: https://doi.org/10.1101/098301; this version posted January 4, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

Frequency bands for EEG analysis were defined using individual alpha frequency (IAF) as follows: theta = [IAF-6 Hz to IAF-2.5 Hz], alpha1 = [IAF-2.5 Hz to IAF], alpha2 = [IAF to IAF+2.5 Hz], beta1 = [IAF+2.5 Hz to 20 Hz], beta2 = [20 Hz to 30 Hz]. The IAF was determined on a 3 min EEG recorded at rest with eyes closed.

Segments of raw EEG recorded during the interval from 500 ms to 6500 ms of the delay period were analyzed. These segments were filtered between 0.5 and 30 Hz, and a 50-Hz notch filter was applied. The segments were subdivided into 2-second epochs. A fast Fourier transformation (FFT) was performed in each epoch. Ocular artefacts were corrected by using independent component analysis (ICA) followed by visual EEG inspection for remaining artefacts. These operations were performed in EEGlab toolbox. Spectral power densities for each frequency bands were calculated using Fieldtrip toolbox.

Spectral power data were statistically analyzed by using two independent mixed-design ANOVAs. The first analysis involved mean power values in four regions of interest (ROI): left (Fp1, F7, F3) and right (Fp2, F8, F4) anterior areas, left (T5, P3, O1) and right (T6, P4, O2) posterior areas. This analysis included a between-subject factor Group (HP, LP) and the within-subject factors Task (retention, manipulation), Load (5 versus 7 letters), Hemisphere (left, right) and Site (anterior, posterior). The second ANOVA of mean power values at the midline (Fz, Cz, Pz) analogous to the previous with factors Group, Task and Load was performed. All statistical calculations were performed by using SPSS package.

Results

Behavioral results

Participants performed with a general mean accuracy of 78.5±0.9%. Mean accuracies for each condition are shown in Fig. 2.

The main effects of Task ($F(1, 63) = 108.1$, $p < 0.0001$, $\eta 2 = .632$) and Load ($F(2, 126) = 49.69$, $p < 0.0001$, $\eta 2 = .441$) as well as their interaction of the factors ($F(2, 126) = 5.606$, $p = 0.005$, $\eta 2 = .082$) were

bioRxiv preprint doi: https://doi.org/10.1101/098301; this version posted January 4, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

obtained. A pairwise comparison between load levels separately for alphabetical and forward conditions showed highly significant differences ($p<0.0001$) for all pairs but two. First, there was no difference between the performance in 5- and 6-letter conditions in the forward order ($p=0.191$). Second, the differences were less pronounced in the comparison between 6 and 7 letters in the alphabetical order ($p=0.011$; not significant after Bonferroni correction). For this reason, and in order to avoid potential problem with sphericity in statistical measures, the 6-letters condition was excluded from the EEG analysis.

The mean performance accuracy in the high and low performance groups was 84.9±0,5% and 71.9±1,1%, respectively ($F(1, 63) = 87.26$, $p < 0.0001$, $\eta 2 = .581$).

Insert Figure 2 about here

Electrophysiological results

Table 1

Results of the ANOVA with the factors Task x Load x Hemisphere x Site x Group.

	Theta			*Alpha1*			*Alpha2*			*Beta1*			*Beta2*		
	F	p	η^2	F	p	η^2	F	p	η^2	F	p	η^2	F	p	η^2
Task	3.631	.061	.054	9.694	**.003**	.133				10.680	**.002**	.145			
Load													4.781	**.033**	.071
Site	14.24	**<.001**	.184	29.38	**<.001**	.318	25.39	**<.001**	.287	16.747	**<.001**	.210	22.75	**<.001**	.265
Hemisphere	7.712	**.007**	.109												
Group							6.143	**.016**	.089						
Site x Hemisphere										5.159	**.027**	.076			
Task x Group				4.763	**.033**	.070									
Task x Load	4.415	**.040**	.065							6.376	**.014**	.092			
Task x Site	8.285	**.005**	.116	5.620	**.021**	.082									
Task x Hemisphere	4.270	**.043**	.063												
Task x Site x Group													5.194	**.026**	.076
Load x Site x Hemisphere	7.586	**.008**	.107	5.363	**.024**	.078									
Task x Site x Hemisphere x Group	9.042	**.004**	.126							5.131	**.027**	.075			

Table 2

Results of the ANOVA with the factors Task x Load x Group for midline sites.

		F	p	η^2
Task	*Theta*	7.685	**.007**	.109
	Alpha1	6.526	**.013**	.094
	Beta1	20.427	**<.001**	.245
	Alpha1	4.715	**.034**	.070
Load x Group	*Theta*	4.465	**.039**	.066
Task x Group	*Beta1*	6.281	**.015**	.091
Task x Load	*Theta*	5.462	**.023**	.080
	Beta1	5.895	**.018**	.086

bioRxiv preprint doi: https://doi.org/10.1101/098301; this version posted January 4, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

General tendencies

Theta

The theta rhythm had lower power in anterior areas in comparison with posterior areas (main effect of Site, see Table 1 for this section). Also, the power was higher over the left than the right hemisphere (main effect of Hemisphere). Furthermore, the theta power decreased with the increasing WM load at all ROIs except the right anterior one (Load x Site x Hemisphere interaction).

Across the whole sample, the theta power tended to be higher in the manipulation task than in the retention task. As depicted in Fig. 3. this effect was more pronounced at anterior than posterior areas (Task x Site interaction) and also more pronounced over the left than the right hemisphere (Task x Hemisphere interaction).

The analysis of midline theta showed higher power in the manipulation task than in the retention task (main effect of Task, see Table 2). Increasing number of the presented letters from 5 to 7 yielded a decrease of theta power in the manipulation task but its increase in the retention task (Task x Load interaction). This interaction was, however, strongly modified by the between-subject factor, as described below in the Section Individual differences-Theta.

Insert Figure 3 about here

Alpha

As expected, alpha1 and alpha2 activity increased in the posterior direction (main effect of Site, see Table 1).

Alpha1 power was lower in the manipulation task than in the retention tasks (main effect of Task). This effect was larger at the posterior than anterior sites (Task x Site interaction).

bioRxiv preprint doi: https://doi.org/10.1101/098301; this version posted January 4, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

Alpha1 activity was suppressed with increasing WM load in each ROI except the right posterior area where alpha1 power increased (Load x Site x Hemisphere interaction).

Beta1

Beta1 power was significantly lower in the anterior than posterior areas (main effect of Site), and lower on the left than right side (main effect of Hemisphere).

As can be seen in Fig. 4, beta1 power increased with the increasing WM load in the manipulation conditions but decreased in the retention conditions (Task x Load interaction). In general, the power was higher in the retention condition than in the manipulation condition (main effect of Task).

Insert Figure 4 about here

Beta2

In contrast to beta1, beta2 power was significantly larger in the anterior than posterior areas (main effect of Site). Increasing WM load led to an increase in beta2 activity (main effect of Load).

Individual differences

Theta

The analysis revealed a four-way interaction between Task, Site, Hemisphere and Group. Additional separate analyses in groups were performed. In the HP group we observed a larger theta power in the manipulation condition than in the retention condition, and the magnitude of this effect was the highest in

bioRxiv preprint doi: https://doi.org/10.1101/098301; this version posted January 4, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

the left anterior area (Task x Site x Hemisphere interaction ($F(1, 31) = 7.605$, $p = 0.01$, $\eta^2 = .197$). No significant effects were found in the LP group.

An ANOVA performed on midline electrodes revealed opposite load dependent changes of the midline theta power in the HP and LP groups. As depicted in Fig. 5, an increase of the number of letters from 5 to 7 was associated with an increase of theta activity in the former group but its decrease in the latter (Load x Group interaction, see Table 1). Fig. 5 shows that the significant Load x Task interaction for the entire sample, described above in Section General tendencies-Theta, is actually produced by the dramatic decrement of the theta power in the most demanding condition (manipulation task, high WM load) in the LP group. Similarly, the triple interaction Load x Site x Hemisphere for the entire sample does not really characterize the entire sample but, like the Load x Task interaction, can be attributed to a disproportionately strong influence of the LP group.

Insert Figure 5 about here

Alpha

As can be seen in Fig. 6, the suppression of the alpha1 power in the manipulation task relative to the retention task was stronger in the HP than the LP group (Task x Group interaction). Alpha2 was generally stronger in the HP than the LP group (main effect of Group).

Insert Figure 6 about here

Beta1

bioRxiv preprint doi: https://doi.org/10.1101/098301; this version posted January 4, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

A significant four-way interaction Task x Site x Hemisphere x Group was obtained and further analyzed for groups and for electrode sites. The first ANOVA yielded a significant Task x Site x Hemisphere interaction ($F(1, 31) = 6.471$, $p < 0.05$, $\eta^2 = .131$) only in the HP group, indicating that the decrease of the beta1 power from the retention task to the manipulation task was more pronounced in the left posterior and the right anterior ROIs. No such effects were observed in the LP group.

The second ANOVA revealed a significant Task x Group interaction in the left posterior ROI ($F(1, 31) = 5,953$, $p < 0.05$, $\eta^2 = .086$), indicating task dependent changes of beta1 power at the left posterior area in the HP group (see Fig. 7).

Insert Figure 7 about here

Beta2

The significant Task x Site x Group interaction (see Table 1) indicates opposite task- and location-related changes in the two groups. The LP group showed higher beta2 activity in the manipulation task at anterior areas but in the retention task at posterior areas, while the opposite held true for the HP group (Fig. 8).

Insert Figure 8 about here

Discussion

General tendencies

Theta and central executive components of WM

bioRxiv preprint doi: https://doi.org/10.1101/098301; this version posted January 4, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

The current study found that increasing WM task complexity and executive control demand were associated with the increase of the frontal theta activity. Increasing theta power in midline and frontal areas during mental manipulations in contrast to the mere retention of memory content is in line with numerous data indicating positive relationships between FMT and cognitive load [3,9–11,28]. Moreover, an increase of FMT in manipulaton tasks as compared with retention tasks was also found in studies whose design was similar to the present one [31–33,52].

In addition, the link between FMT and the activation of the anterior cingulate cortex (ACC) and the medial prefrontal cortex (mPFC) was repeatedly proven by simultaneous EEG-fMRI recordings as well as by direct electrophysiological recordings in monkeys [53–56]. The ACC and the mPFC are active during memory processes, WM performance, and executive control [57–59].

We assume that the increment of FMT (supposedly indicating the activation of the ACC) with increasing WM demands is related to increasing involvement of executive processes. However, it should be noted that FMT reflects not pure memory processes per se but more likely the allocation of cortical resources depending on features of the task [3,59,60]. One may speculate that increasing demands for executive control during manipulation of information in WM engage a widely distributed network whose main components are the prefrontal cortex and the ACC.

Alpha1 and the storage components of WM

As compared with the retention condition, manipulation of stimuli in WM was associated with distributed suppression of alpha1 activity. There is an empirically well supported hypothesis that desynchronization of low alpha is a nonspecific cortical response that can be observed during various cognitive operations [9,38,61] including maintaining information in WM [53,62,63]. In addition to this non-specificity model, however, more specific hypotheses about the dynamics of alpha exist. Thus, the

bioRxiv preprint doi: https://doi.org/10.1101/098301; this version posted January 4, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

alpha synchronization in posterior areas during the maintenance of actual information may reflect active inhibition to protect these areas from reorienting to new irrelevant information processing [28,42]. It is plausible that the temporary storage components of WM play the key role in a successful maintenance of 7 letters relative to 5 letters. It might be suggested that when the volume of information maintained in the temporary storage approaches the putative capacity limit (7+-2) the central executive should actively inhibit irrelevant information. The observed asymmetry of alpha1 power at the posterior area agrees with the previous studies of WM and short-term memory [9,28,54,64,65].

Beta1 and manipulation of information in WM

Task-related decrement of beta1 power found in this study was quite similar to the effect reported by Berger et al. [32] who also compared manipulation versus retention conditions. This effect may be explained by the conception of Engel & Fries [66] that, applied to the present experiment, suggests that the decrease of beta1 power takes place during updating or manipulating information in WM as well as during retrieval of information from long term memory and encoding it in WM. The desynchronization of the beta1 rhythm can be attributed to the sequential updating of the WM content during mental alphabetizing of the letters. This process also involves addressing the long term memory where the alphabet is stored.

Load-dependent changes in beta1 power were observed only in the manipulation condition. We hypothesize that manipulation is underpinned by two independent temporal buffers: the first one is the final storage for modified items after the manipulations, whereas the second one serves as a workspace for the remaining to-be-modified items. Perhaps, there are even two different beta1 rhythms that overlap in frequency but reflect different sub-processes in WM [67]. The first rhythm supports the activity of the first buffer (“store”), and the second rhythm, that of the second buffer (“workspace”). Synchronization of the former maintains the active state of the engram and protects it from irrelevant information. Weiss &

bioRxiv preprint doi: https://doi.org/10.1101/098301; this version posted January 4, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

Rappelsberger [68] demonstrated a gradual increase of beta1 activity in response to sequential filling of WM by words. Research conducted by Leiberg, Lutzenberger, & Kaiser [69] also showed a load-dependent increase of beta1 activity. At the same time desynchronization of the other beta1 rhythm reflects the retrieval from long term memory and encoding to WM. In other words, desynchronization of the latter beta1 rhythm reflects manipulations of objects in "workspace" for their subsequent transfer to "store".

Our hypothesis also entails that the lack of beta1 desynchronization during the encoding process indicates a disruption of memory formation. Recently, Hanslmayr, Matuschek, & Fellner [70] found a negative effect of transcranial magnetic stimulation (TMS) of the left inferior frontal gyrus at beta1 frequency (18.7 Hz) on memory performance in a word-list learning task. Furthermore, a study [44] performed on monkeys demonstrated desynchronization of beta activity during updating of WM content but synchronization of beta activity during retention.

Probably, in the retention condition the "workspace" buffer is minimally involved. It may work at the beginning of the delay period when sequentially and quickly presented information is encoded. Thus Zanto & Gazzaley [71] found the desynchronization of beta1 rhythm during the first 1250 ms of the 4-s delay period but the synchronization from 1500 ms to the end of the delay. In the current study, the delay periods during maintaining and manipulation of 5 and 7 letters could be different due to a longer presentation time (3 seconds). Therefore, the recombination of 5 letters to the alphabetical order could already start during stimulus presentation and continue only in the "workspace" buffer without addressing the "store" buffer. When the recombination process is finished, the result is transferred to the "store" buffer and kept there until the probe is presented. The "store" buffer in this case prevents possible interference of other stimuli and maintains the actual state of the engram until the moment when its content is requested. When a longer stimulus set is memorized (i.e., 7 letters) a plausible strategy is to memorize the initial letters set and to transfer it into the "store" buffer. If this strategy is used, recombination may start after the stimuli have disappeared from the screen. During this period, both buffers are actively involved: the "store" buffer is keeping the initial set, while recombination is carried out in the "workspace" buffer. When the

bioRxiv preprint doi: https://doi.org/10.1101/098301; this version posted January 4, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

recombination is finished the information transfers to the "store" and updates its content. This assumed information return to, and updating of, the "store" buffer would explain the increase of beta1 power from 5- to 7-letter condition in the manipulation task.

Beta2 and amount of information in WM

Beta2 power increased with the increasing WM load and did not significantly depend on the type of the task.

Dissociations between the lower (13-20 Hz) and upper (25-30 Hz) beta were demonstrated earlier in a study of Shahin, Picton, & Miller [72]. The authors concluded that the increment of the upper beta may reflect maintaining verbal stimuli in auditory memory. The maintenance of stimuli in WM was also suggested to cause synchronization of beta2 (~20-30 Hz) in two different tasks [73,74]. Spitzer et al. [74] assumed that the upper beta activity is directly related to the quantity of supramodal abstract information. The significant effect of Load on beta2 power found in the present study is in line with this interpretation.

Individual differences

Theta

The task-related increment of theta power in the left anterior area was found only in the HP group. This may be related to more effective manipulations supported by the hippocampus and language cortex. Previous WM studies demonstrated a relationship between the hippocampal activity and the theta rhythm [75,76]. In animal studies, the synchronized activity of the prefrontal cortex and the hippocampus crucially determined the accuracy in WM tasks [77,78]. The prefrontal cortex is hypothesized to be supported under excessive WM load by the medial temporal lobe related to long term memory [79–81].

bioRxiv preprint doi: https://doi.org/10.1101/098301; this version posted January 4, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

The activation of the left prefrontal cortex including the inferior frontal gyrus (IFG) and Broca's area was found in verbal tasks during executive processes functions [55,82,83]. Simultaneous EEG / fMRI recording in a modified Sternberg task revealed a load-dependent increase of left IFG activation and the theta rhythm [55]. Similar results were obtained by Chee & Choo [84] in a WM task. We suppose that the left-hemispheric accentuation of the theta rhythm represents more effective information exchange between short- and long-term memory storage in the HP group.

Group differences were not only task-dependent but also load-dependent. The HP group demonstrated a gradual increase of theta power at midline, reaching its peak in the most demanding condition: manipulation task with 7 letters. In contrast, the LP group exhibited a sharp drop of theta power in this condition after a maximum in the condition of moderate difficulty: manipulation with 5 letters. Since previous studies of EEG correlates of individual differences in WM were limited to moderate difficulty, we can state that our findings are fully consistent with the previous ones, where the theta activity always increased with memory load [1,3,4,9–11]. However, the most difficult task resulted in a more complex change of theta activity that has not been observed so far.

One may speculate that reaching the individual's WM capacity limit is accompanied by a crucial deficit of attentional resources. Post-experimental reports suggest that most participants formulated their task as "to remember all letters if possible", but possibly, some LP participants in the most difficult condition changed the task to "to remember at least some letters". Alternatively, some subjects may have switched strategy to "remember the first few letters with regard to position" in the forward task and the "first few letters with regard to alphabetical order" in the alphabetical task. This post-hoc hypothesis was tested by an analysis of behavioral results with regards to the position of the probe letter. The factor Position was taken with 2 levels (the first two versus the last 2 letters for 5-letters conditions, or the first three versus the last 3 letters for 7-letters conditions). We found two significant interactions between Position and Group: Position x Group ($F(1, 63) = 6.022$, $p = 0.017$, $\eta^2 = .087$) and Position x Task x Load x Group ($F(1, 63) = 3.183$, $p = 0.045$, $\eta^2 = .048$). Unfortunately, due to the post-hoc nature of this effect we could not

bioRxiv preprint doi: https://doi.org/10.1101/098301; this version posted January 4, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

perform the EEG analysis with the factor Position, because we did not have a sufficient statistical power for this unplanned comparison.

Another explanation might be the loss of motivation in LP participants in the most challenging condition. This hypothesis, however, would predict a particularly poor performance of LP participants in the manipulation task with 7 letters. This disagrees with the observed data indicating nearly equal performance differences between LP and HP participants in all conditions (see Fig. 5). From our point of view, the strategy change hypothesis can better integrate this fact that the loss-of-motivation hypothesis.

Also Jaeggi et al. [2] came on the basis of their fMRI study to the same conclusion concerning the suboptimal strategies used by LP subjects in WM tasks. In that study, LP participants showed a positive correlation between task complexity and the amount of the broad activation in the frontal cortex. Obviously, the most challenging condition leads to the widely distributed engagement of the prefrontal cortex and results in the lack of neural resources for activation of the ACC necessary for the executive control of WM.

Alpha

In the development of the cortical idling hypothesis, [85] proposed that the increasing alpha activity during cognitive processing is related to the allocation of attentional resources by inhibition of the cortical areas irrelevant to the current task [42,86,87]. In this context alpha rhythm plays the role of an information flow filter.

It is well known that WM is one of the main components of general intelligence [88,89]. Accordingly, the degree of alpha desynchronization in semantic memory task is positively related to intelligence [90]. Similar correlations between IQ and alpha power were observed in the resting state [91,92]. We suppose that stronger alpha power may reflect a higher level of readiness to perceive relevant information. Therefore, HP individuals have potentially more resourceful visual cortex and manage the tasks better [61].

bioRxiv preprint doi: https://doi.org/10.1101/098301; this version posted January 4, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

Beta1

The main result was a stronger desynchronization of beta1 rhythm in the HP group in the manipulation condition in the left posterior area. An important role of the superior parietal cortex in flexible redistribution of attentional resources was demonstrated in several studies [93–96]. In terms of the two-buffer model (see above, Section General tendencies-Beta1), one may suggest that HP individuals are better able to shift their attention between the store of the originally presented set and the workspace where they work with the symbols. This might allow them to perform manipulations in the "workspace" buffer not spending too much resources for maintaining information in the "store" buffer.

Beta2

In the manipulation task, beta2 power increased in the HP group in the anterior areas, but in the LP group in the posterior areas. As we do not know any comparable data in the literature, only a very preliminary explanation can be proposed. Beta2 is the EEG index that may most simply be designated as "activation". We believe, therefore, that changes in beta2 activity are not related to mental processes as such, but rather to the general volume of information necessarily used in these processes. This volume is expected to be larger in the manipulation task than in the retention task because during manipulation one has to work with at least two stimulus sets: the one that should be manipulated with and the one that results from the manipulation. The increase of frontal activity in HP participants may, therefore, reflect their ability to process a larger amount of information, whereas the heightened activity of sensory regions in LP subjects appears to reflect their need to frequently address the original stimulus set.

General discussion

bioRxiv preprint doi: https://doi.org/10.1101/098301; this version posted January 4, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

In general, the obtained results allow us to make several claims about possible factors contributing, at the individual level, to effective verbal WM performance:

firstly, a higher state of readiness to process relevant and to inhibit irrelevant information and related larger alpha power;

secondly, stronger engagement of the left prefrontal cortex and the hippocampus; this factor can underlie efficient maintaining and manipulating information in WM due to a fast exchange of information between long term and working memory;

thirdly, an energy efficient strategy for distribution of frontal resources in order to maintain the necessary level of activity of the ACC;

finally, activation of the ACC and the related executive functions is decisive for successful manipulations of content in WM, simultaneous maintaining information about initial properties of stimuli and efficiently shifting attention between these cognitive operations.

Limitations

We have to acknowledge at least two limitations of the present study. Firstly, the results may be affected by the homogeneity of the sample in respect to gender (i.e., females). A gender based analysis will be the matter of a subsequent report Secondly, our putative explanation hypotheses suggested in the Discussion above have neuroanatomical implications, i.e., they presume the activity of certain brain structures such as the ACC. To test these hypotheses, a larger number of electrodes should be used in future studies, which will allow a more precise assessment of the spatial distribution of the obtained effects.

Conclusions

bioRxiv preprint doi: https://doi.org/10.1101/098301; this version posted January 4, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

1. In accordance with many previous studies, we expected to find significant WM-related changes in alpha and theta frequency bands. This hypothesis was only partially supported by the data. Significant effects were found in all analyzed frequency bands from theta to high beta, indicating that our knowledge about the neural basis of WM is not comprehensive.
2. The hypothesis about a strong participation of the frontal theta rhythm in WM processes was confirmed. The novel finding was, however, different dynamics of frontal theta in HP and LP groups.
3. When starting the study, we believed that some important findings can have been missed in the previous experiments because they used only tasks of low to average difficulty. Therefore, we predicted important intergroup variation in EEG pattern in the most challenging condition. This prediction was confirmed. The most pronounced differences between individuals with high and low WM performance, in terms of the oscillatory activity in several frequency ranges, were observed in the manipulation task with 7 letters, which is a very difficult condition that for many individuals might exceed their limits. Particularly, this condition resulted in a more complex change of theta activity than just an increase with WM load, which has not been observed so far. Including greater variety of experimental conditions and groups to the WM research agenda seems beneficial.
4. Finally, we expected a stronger effect of executive WM components as compared with storage components. The data put this hypothesis in question. Firstly, the difference in performance between LP and HP participants was nearly equal in retention (weak executive control demands) and manipulation (much higher executive control demands) conditions. Secondly, task and site dependent group differences were found in each explored frequency bands including anterior theta and posterior alpha activity. In some studies these two responses were interpreted as reflections of executive and storage components of WM, respectively [5,6]. Although there is an alternative interpretation on the basis of cross-frequency coupling [7,8], all these observations together may

bioRxiv preprint doi: https://doi.org/10.1101/098301; this version posted January 4, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

indicate that the two components of WM are equally important for WM performance at the individual level. More studies are needed to clarify this issue

Declarations

Abbreviations

WM: working memory

HP: high performance

LP: low performance

tACS: transcranial alternating current stimulation

FMT: frontal midline theta rhythm

EEG: electroencephalography

EOG: electrooculography

IAF: individual alpha frequency

FFT: fast Fourier transformation

ICA: independent component analysis

ROI: region of interest

SEM: standard error of the mean

IFG: inferior frontal gyrus

fMRI: functional magnetic resonance imaging

ACC: anterior cingulate cortex

IQ: intelligence quotient

ANOVA: analysis of variance

Ethics approval and consent to participate

bioRxiv preprint doi: https://doi.org/10.1101/098301; this version posted January 4, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

Informed consent was obtained from all subjects prior to the study. The study was approved by the Ural Federal University Ethics Committee.

Consent for publication

Not applicable.

Availability of data and materials

The datasets analyzed during the current study is available from the corresponding author on reasonable request.

Competing interests

The authors declare that they have no competing interests.

Funding

We acknowledge support by the Deutsche Forschungsgemeinschaft and Open Access Publishing Fund of University of Tübingen

Authors' contributions

YGP: conceived of the study, designed the experimental paradigm, carried out the recording of the data, performed the statistical analysis and drafted the manuscript

BK: contributed to the discussion, and to the preparation of the manuscript

All authors read and approved the final manuscript.

Acknowledgements

Not applicable.

bioRxiv preprint doi: https://doi.org/10.1101/098301; this version posted January 4, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

600 **References**

601

602 1. Daffner KR, Chong H, Sun X, Tarbi EC, Riis JL, McGinnis SM, et al. Mechanisms Underlying Age-
603 and Performance-related Differences in Working Memory. J. Cogn. Neurosci. 2011;23:1298–314.

604 2. Jaeggi SM, Buschkuehl M, Etienne A, Ozdoba C, Perrig WJ, Nirkko AC. On how high performers
605 keep cool brains in situations of cognitive overload. Cogn. Affect. Behav. Neurosci. 2007;7:75–89.

606 3. Onton J, Delorme A, Makeig S. Frontal midline EEG dynamics during working memory. NeuroImage.
607 2005;27:341–56.

608 4. Pesonen M, Hämäläinen H, Krause CM. Brain oscillatory 4–30 Hz responses during a visual n-back
609 memory task with varying memory load. Brain Res. 2007;1138:171–7.

610 5. Kawasaki M, Kitajo K, Yamaguchi Y. Dynamic links between theta executive functions and alpha
611 storage buffers in auditory and visual working memory. Eur. J. Neurosci. 2010;31:1683–9.

612 6. Dimitriadis SI, Sun Y, Kwok K, Laskaris NA, Thakor N, Bezerianos A. Cognitive Workload
613 Assessment Based on the Tensorial Treatment of EEG Estimates of Cross-Frequency Phase Interactions.
614 Ann. Biomed. Eng. 2015;43:977–89.

615 7. Axmacher N, Henseler MM, Jensen O, Weinreich I, Elger CE, Fell J. Cross-frequency coupling
616 supports multi-item working memory in the human hippocampus. Proc. Natl. Acad. Sci. 2010;107:3228–
617 33.

618 8. Canolty RT, Knight RT. The functional role of cross-frequency coupling. Trends Cogn. Sci.
619 2010;14:506–515.

bioRxiv preprint doi: https://doi.org/10.1101/098301; this version posted January 4, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

620 9. Gevins A, Smith ME, McEvoy L, Yu D. High-resolution EEG mapping of cortical activation related to
621 working memory: effects of task difficulty, type of processing, and practice. Cereb. Cortex. 1997;7:374–
622 385.

623 10. Itthipuripat S, Wessel JR, Aron AR. Frontal theta is a signature of successful working memory
624 manipulation. Exp. Brain Res. 2012;224:255–62.

625 11. Missonnier P, Deiber M-P, Gold G, Millet P, Pun MG-F, Fazio-Costa L, et al. Frontal theta event-
626 related synchronization: comparison of directed attention and working memory load effects. J. Neural
627 Transm. Springer; 2006;113:1477–86.

628 12. Daneman M, Merikle PM. Working memory and language comprehension: A meta-analysis. Psychon.
629 Bull. Rev. 1996;3:422–33.

630 13. D'Esposito M. From cognitive to neural models of working memory. Philos. Trans. R. Soc. B Biol.
631 Sci. 2007;362:761–72.

632 14. Hyun J-S, Luck SJ. Visual working memory as the substrate for mental rotation. Psychon. Bull. Rev.
633 2007;14:154–158.

634 15. Baddeley A. Working Memory: Theories, Models, and Controversies. Annu. Rev. Psychol.
635 2012;63:1–29.

636 16. Baddeley A. Working memory: looking back and looking forward. Nat. Rev. Neurosci. 2003;4:829–
637 39.

638 17. Engle RW, Tuholski SW, Laughlin JE, Conway AR. Working memory, short-term memory, and
639 general fluid intelligence: a latent-variable approach. J. Exp. Psychol. Gen. 1999;128:309.

bioRxiv preprint doi: https://doi.org/10.1101/098301; this version posted January 4, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

640 18. Postle BR. Working memory as an emergent property of the mind and brain. Neuroscience.
641 2006;139:23–38.

642 19. Nee DE, Brown JW, Askren MK, Berman MG, Demiralp E, Krawitz A, et al. A Meta-analysis of
643 Executive Components of Working Memory. Cereb. Cortex. 2013;23:264–82.

644 20. Cohen JD, Perlstein WM, Braver TS, Nystrom LE, Noll DC, Jonides J, et al. Temporal dynamics of
645 brain activation during a working memory task. Nature. 1997;386:604–8.

646 21. Edin F, Klingberg T, Johansson P, McNab F, Tegnér J, Compte A. Mechanism for top-down control
647 of working memory capacity. Proc. Natl. Acad. Sci. 2009;106:6802–6807.

648 22. Klingberg T, O'Sullivan BT, Roland PE. Bilateral activation of fronto-parietal networks by
649 incrementing demand in a working memory task. Cereb. Cortex. 1997;7:465–471.

650 23. Linden DEJ, Bittner RA, Muckli L, Waltz JA, Kriegeskorte N, Goebel R, et al. Cortical capacity
651 constraints for visual working memory: dissociation of fMRI load effects in a fronto-parietal network.
652 NeuroImage. 2003;20:1518–30.

653 24. Palva JM, Monto S, Kulashekhar S, Palva S. Neuronal synchrony reveals working memory networks
654 and predicts individual memory capacity. Proc. Natl. Acad. Sci. 2010;107:7580–5.

655 25. Ekman M, Fiebach CJ, Melzer C, Tittgemeyer M, Derrfuss J. Different Roles of Direct and Indirect
656 Frontoparietal Pathways for Individual Working Memory Capacity. J. Neurosci. 2016;36:2894–903.

657 26. Buzsaki G. Neuronal Oscillations in Cortical Networks. Science. 2004;304:1926–9.

658 27. Aftanas LI, Golocheikine S a. Human anterior and frontal midline theta and lower alpha reflect
659 emotionally positive state and internalized attention: high-resolution EEG investigation of meditation.
660 Neurosci. Lett. 2001;310:57–60.

bioRxiv preprint doi: https://doi.org/10.1101/098301; this version posted January 4, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

661 28. Jensen O, Tesche CD. Frontal theta activity in humans increases with memory load in a working
662 memory task. Eur. J. Neurosci. 2002;15:1395–1399.

663 29. Sauseng P, Klimesch W, Schabus M, Doppelmayr M. Fronto-parietal EEG coherence in theta and
664 upper alpha reflect central executive functions of working memory. Int. J. Psychophysiol. 2005;57:97–
665 103.

666 30. Sauseng P, Griesmayr B, Freunberger R, Klimesch W. Control mechanisms in working memory: A
667 possible function of EEG theta oscillations. Neurosci. Biobehav. Rev. 2010;34:1015–22.

668 31. Berger B, Minarik T, Griesmayr B, Stelzig-Schoeler R, Aichhorn W, Sauseng P. Brain Oscillatory
669 Correlates of Altered Executive Functioning in Positive and Negative Symptomatic Schizophrenia
670 Patients and Healthy Controls. Psychopathology. 2016;705.

671 32. Berger B, Omer S, Minarik T, Sterr A, Sauseng P. Interacting Memory Systems—Does EEG Alpha
672 Activity Respond to Semantic Long-Term Memory Access in a Working Memory Task? Biology.
673 2014;4:1–16.

674 33. Griesmayr B, Gruber WR, Klimesch W, Sauseng P. Human frontal midline theta and its
675 synchronization to gamma during a verbal delayed match to sample task. Neurobiol. Learn. Mem.
676 2010;93:208–15.

677 34. Cooper PS, Wong ASW, Fulham WR, Thienel R, Mansfield E, Michie PT, et al. Theta frontoparietal
678 connectivity associated with proactive and reactive cognitive control processes. NeuroImage.
679 2015;108:354–63.

680 35. Sarnthein J, Petsche H, Rappelsberger P, Shaw GL, Von Stein A. Synchronization between prefrontal
681 and posterior association cortex during human working memory. Proc. Natl. Acad. Sci. 1998;95:7092–
682 7096.

bioRxiv preprint doi: https://doi.org/10.1101/098301; this version posted January 4, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

683 36. Wu X, Chen X, Li Z, Han S, Zhang D. Binding of verbal and spatial information in human working
684 memory involves large-scale neural synchronization at theta frequency. NeuroImage. 2007;35:1654–62.

685 37. Polanía R, Nitsche MA, Korman C, Batsikadze G, Paulus W. The Importance of Timing in
686 Segregated Theta Phase-Coupling for Cognitive Performance. Curr. Biol. 2012;22:1314–8.

687 38. Klimesch W. Alpha-band oscillations, attention, and controlled access to stored information. Trends
688 Cogn. Sci. 2012;16:606–617.

689 39. Sauseng P, Klimesch W, Heise KF, Gruber WR, Holz E, Karim AA, et al. Brain Oscillatory
690 Substrates of Visual Short-Term Memory Capacity. Curr. Biol. 2009;19:1846–52.

691 40. Tuladhar AM, Huurne N ter, Schoffelen J-M, Maris E, Oostenveld R, Jensen O. Parieto-occipital
692 sources account for the increase in alpha activity with working memory load. Hum. Brain Mapp.
693 2007;28:785–92.

694 41. Jensen O, Mazaheri A. Shaping Functional Architecture by Oscillatory Alpha Activity: Gating by
695 Inhibition. Front. Hum. Neurosci. [Internet]. 2010 [cited 2016 May 23];4. Available from:
696 http://journal.frontiersin.org/article/10.3389/fnhum.2010.00186/abstract

697 42. Klimesch W, Sauseng P, Hanslmayr S. EEG alpha oscillations: The inhibition–timing hypothesis.
698 Brain Res. Rev. 2007;53:63–88.

699 43. Deiber M-P, Missonnier P, Bertrand O, Gold G, Fazio-Costa L, Ibanez V, et al. Distinction between
700 perceptual and attentional processing in working memory tasks: a study of phase-locked and induced
701 oscillatory brain dynamics. Cogn. Neurosci. J. Of. 2007;19:158–172.

702 44. Siegel M, Warden MR, Miller EK. Phase-dependent neuronal coding of objects in short-term
703 memory. Proc. Natl. Acad. Sci. 2009;106:21341–21346.

bioRxiv preprint doi: https://doi.org/10.1101/098301; this version posted January 4, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

704 45. Tallon-Baudry C, Bertrand O, Peronnet F, Pernier J. Induced γ-Band Activity during the Delay of a
705 Visual Short-Term Memory Task in Humans. J. Neurosci. 1998;18:4244–54.

706 46. Barrett LF, Tugade MM, Engle RW. Individual Differences in Working Memory Capacity and Dual-
707 Process Theories of the Mind. Psychol. Bull. 2004;130:553–73.

708 47. Engle RW, Kane MJ. Executive attention, working memory capacity, and a two-factor theory of
709 cognitive control. Psychol. Learn. Motiv. 2004;44:145–200.

710 48. Unsworth N, Spillers GJ. Working memory capacity: Attention control, secondary memory, or both?
711 A direct test of the dual-component model. J. Mem. Lang. 2010;62:392–406.

712 49. Brouwer A-M, Hogervorst MA, van Erp JBF, Heffelaar T, Zimmerman PH, Oostenveld R. Estimating
713 workload using EEG spectral power and ERPs in the n-back task. J. Neural Eng. 2012;9:045008.

714 50. Dong S, Reder LM, Yao Y, Liu Y, Chen F. Individual differences in working memory capacity are
715 reflected in different ERP and EEG patterns to task difficulty. Brain Res. 2015;1616:146–56.

716 51. Gevins A, Smith ME. Neurophysiological Measures of Working Memory and Individual Differences
717 in Cognitive Ability and Cognitive Style. Cereb. Cortex. 2000;10:829–39.

718 52. Griesmayr B, Berger B, Stelzig-Schoeler R, Aichhorn W, Bergmann J, Sauseng P. EEG theta phase
719 coupling during executive control of visual working memory investigated in individuals with
720 schizophrenia and in healthy controls. Cogn. Affect. Behav. Neurosci. 2014;14:1340–55.

721 53. Meltzer JA, Negishi M, Mayes LC, Constable RT. Individual differences in EEG theta and alpha
722 dynamics during working memory correlate with fMRI responses across subjects. Clin. Neurophysiol.
723 2007;118:2419–2436.

bioRxiv preprint doi: https://doi.org/10.1101/098301; this version posted January 4, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

724 54. Michels L, Bucher K, Lüchinger R, Klaver P, Martin E, Jeanmonod D, et al. Simultaneous EEG-fMRI
725 during a Working Memory Task: Modulations in Low and High Frequency Bands. PLoS ONE.
726 2010;5:e10298.

727 55. Scheeringa R, Petersson KM, Oostenveld R, Norris DG, Hagoort P, Bastiaansen MCM. Trial-by-trial
728 coupling between EEG and BOLD identifies networks related to alpha and theta EEG power increases
729 during working memory maintenance. NeuroImage. 2009;44:1224–38.

730 56. Tsujimoto T, Shimazu H, Isomura Y, Sasaki K. Theta Oscillations in Primate Prefrontal and Anterior
731 Cingulate Cortices in Forewarned Reaction Time Tasks. J. Neurophysiol. 2010;103:827–43.

732 57. Bush G, Luu P, Posner MI. Cognitive and emotional influences in anterior cingulate cortex. Trends
733 Cogn. Sci. 2000;4:215–222.

734 58. Niendam TA, Laird AR, Ray KL, Dean YM, Glahn DC, Carter CS. Meta-analytic evidence for a
735 superordinate cognitive control network subserving diverse executive functions. Cogn. Affect. Behav.
736 Neurosci. 2012;12:241–68.

737 59. Shenhav A, Botvinick MM, Cohen JD. The Expected Value of Control: An Integrative Theory of
738 Anterior Cingulate Cortex Function. Neuron. 2013;79:217–40.

739 60. Sauseng P, Hoppe J, Klimesch W, Gerloff C, Hummel FC. Dissociation of sustained attention from
740 central executive functions: local activity and interregional connectivity in the theta range. Eur. J.
741 Neurosci. 2007;25:587–93.

742 61. Klimesch W, Vogt F, Doppelmayr M. Interindividual differences in alpha and theta power reflect
743 memory performance. Intelligence. 1999;27:347–362.

744 62. Maurer U, Brem S, Liechti M, Maurizio S, Michels L, Brandeis D. Frontal Midline Theta Reflects
745 Individual Task Performance in a Working Memory Task. Brain Topogr. 2015;28:127–34.

bioRxiv preprint doi: https://doi.org/10.1101/098301; this version posted January 4, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

746 63. Michels L, Moazami-Goudarzi M, Jeanmonod D, Sarnthein J. EEG alpha distinguishes between
747 cuneal and precuneal activation in working memory. NeuroImage. 2008;40:1296–310.

748 64. Babiloni C, Babiloni F, Carducci F, Cappa SF, Cincotti F, Del Percio C, et al. Human cortical
749 rhythms during visual delayed choice reaction time tasks. Behav. Brain Res. 2004;153:261–71.

750 65. Liu Z-X, Glizer D, Tannock R, Woltering S. EEG alpha power during maintenance of information in
751 working memory in adults with ADHD and its plasticity due to working memory training: A randomized
752 controlled trial. Clin. Neurophysiol. 2016;127:1307–20.

753 66. Engel AK, Fries P. Beta-band oscillations—signalling the status quo? Curr. Opin. Neurobiol.
754 2010;20:156–65.

755 67. Weiss S, Mueller HM. "Too Many betas do not Spoil the Broth": The Role of Beta Brain Oscillations
756 in Language Processing. Front. Psychol. [Internet]. 2012 [cited 2016 May 14];3. Available from:
757 http://journal.frontiersin.org/article/10.3389/fpsyg.2012.00201/abstract

758 68. Weiss S, Rappelsberger P. Long-range EEG synchronization during word encoding correlates with
759 successful memory performance. Cogn. Brain Res. 2000;9:299–312.

760 69. Leiberg S, Lutzenberger W, Kaiser J. Effects of memory load on cortical oscillatory activity during
761 auditory pattern working memory. Brain Res. 2006;1120:131–40.

762 70. Hanslmayr S, Matuschek J, Fellner M-C. Entrainment of Prefrontal Beta Oscillations Induces an
763 Endogenous Echo and Impairs Memory Formation. Curr. Biol. 2014;24:904–9.

764 71. Zanto TP, Gazzaley A. Neural Suppression of Irrelevant Information Underlies Optimal Working
765 Memory Performance. J. Neurosci. 2009;29:3059–66.

bioRxiv preprint doi: https://doi.org/10.1101/098301; this version posted January 4, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

766 72. Shahin AJ, Picton TW, Miller LM. Brain oscillations during semantic evaluation of speech. Brain
767 Cogn. 2009;70:259–66.

768 73. Spitzer B, Blankenburg F. Supramodal Parametric Working Memory Processing in Humans. J.
769 Neurosci. 2012;32:3287–95.

770 74. Spitzer B, Gloel M, Schmidt TT, Blankenburg F. Working Memory Coding of Analog Stimulus
771 Properties in the Human Prefrontal Cortex. Cereb. Cortex. 2014;24:2229–36.

772 75. Benchenane K, Tiesinga PH, Battaglia FP. Oscillations in the prefrontal cortex: a gateway to memory
773 and attention. Curr. Opin. Neurobiol. 2011;21:475–85.

774 76. Sammer G, Blecker C, Gebhardt H, Bischoff M, Stark R, Morgen K, et al. Relationship between
775 regional hemodynamic activity and simultaneously recorded EEG-theta associated with mental
776 arithmetic-induced workload. Hum. Brain Mapp. 2007;28:793–803.

777 77. Hyman JM, Zilli EA, Paley AM, Hasselmo ME. Working Memory Performance Correlates with
778 Prefrontal-Hippocampal Theta Interactions but not with Prefrontal Neuron Firing Rates. Front. Integr.
779 Neurosci. [Internet]. 2010 [cited 2016 May 26];4. Available from:
780 http://www.ncbi.nlm.nih.gov/pmc/articles/PMC2861479/

781 78. Jones MW, Wilson MA. Theta Rhythms Coordinate Hippocampal–Prefrontal Interactions in a Spatial
782 Memory Task. PLOS Biol. 2005;3:e402.

783 79. Cashdollar N, Malecki U, Rugg-Gunn FJ, Duncan JS, Lavie N, Duzel E. Hippocampus-dependent
784 and-independent theta-networks of active maintenance. Proc. Natl. Acad. Sci. 2009;106:20493–20498.

785 80. Eckart C, Fuentemilla L, Bauch EM, Bunzeck N. Dopaminergic stimulation facilitates working
786 memory and differentially affects prefrontal low theta oscillations. NeuroImage. 2014;94:185–92.

bioRxiv preprint doi: https://doi.org/10.1101/098301; this version posted January 4, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

787 81. Jeneson A, Squire LR. Working memory, long-term memory, and medial temporal lobe function.
788 Learn. Mem. 2011;19:15–25.

789 82. Nelson J, Reuter-Lorenz PA, Persson J, Sylvester C-YC, Jonides J. Mapping interference resolution
790 across task domains: A shared control process in left inferior frontal gyrus. Brain Res. 2009;1256:92–100.

791 83. Zhang JX, Feng C-M, Fox PT, Gao J-H, Tan LH. Is left inferior frontal gyrus a general mechanism
792 for selection? NeuroImage. 2004;23:596–603.

793 84. Chee MWL, Choo WC. Functional Imaging of Working Memory after 24 Hr of Total Sleep
794 Deprivation. J. Neurosci. 2004;24:4560–7.

795 85. Pfurtscheller G, Stancak A, Neuper C. Event-related synchronization (ERS) in the alpha band—an
796 electrophysiological correlate of cortical idling: a review. Int. J. Psychophysiol. 1996;24:39–46.

797 86. Brunia CHM, Van Boxtel GJM. Wait and see. Int. J. Psychophysiol. Elsevier; 2001;43:59–75.

798 87. Pfurtscheller G, Neuper C, Flotzinger D, Pregenzer M. EEG-based discrimination between
799 imagination of right and left hand movement. Electroencephalogr. Clin. Neurophysiol. Elsevier;
800 1997;103:642–51.

801 88. Conway AR, Cowan N, Bunting MF, Therriault DJ, Minkoff SR. A latent variable analysis of
802 working memory capacity, short-term memory capacity, processing speed, and general fluid intelligence.
803 Intelligence. 2002;30:163–183.

804 89. Kane MJ, Hambrick DZ, Conway ARA. Working Memory Capacity and Fluid Intelligence Are
805 Strongly Related Constructs: Comment on Ackerman, Beier, and Boyle (2005). Psychol. Bull.
806 2005;131:66–71.

bioRxiv preprint doi: https://doi.org/10.1101/098301; this version posted January 4, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

807 90. Doppelmayr M, Klimesch W, Hödlmoser K, Sauseng P, Gruber W. Intelligence related upper alpha
808 desynchronization in a semantic memory task. Brain Res. Bull. 2005;66:171–7.

809 91. Doppelmayr M, Klimesch W, Stadler W, Poellhuber D, Heine C. EEG alpha power and intelligence.
810 Intelligence. 2002;30:289–302.

811 92. Jaušovec N. Differences in EEG alpha activity related to giftedness. Intelligence. 1996;23:159–173.

812 93. Koenigs M, Barbey AK, Postle BR, Grafman J. Superior Parietal Cortex Is Critical for the
813 Manipulation of Information in Working Memory. J. Neurosci. 2009;29:14980–6.

814 94. Molenberghs P, Mesulam MM, Peeters R, Vandenberghe RRC. Remapping Attentional Priorities:
815 Differential Contribution of Superior Parietal Lobule and Intraparietal Sulcus. Cereb. Cortex.
816 2007;17:2703–12.

817 95. Shomstein S, Yantis S. Control of Attention Shifts between Vision and Audition in Human Cortex. J.
818 Neurosci. 2004;24:10702–6.

819 96. Yantis S, Schwarzbach J, Serences JT, Carlson RL, Steinmetz MA, Pekar JJ, et al. Transient neural
820 activity in human parietal cortex during spatial attention shifts. Nat. Neurosci. 2002;5:995–1002.

821
822
823
824
825
826
827
828

bioRxiv preprint doi: https://doi.org/10.1101/098301; this version posted January 4, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

829

830

831 **Figure Legends**

832 Fig. 1 Examples of the trials.

833 Fig. 2 Mean accuracy in different WM tasks and conditions. Notes. 5R, 6R, 7R – memorizing 5, 6, or 7
834 letters in forward order (Retention condition); 5M, 6M, 7M – memorizing 5, 6, or 7 letters in alphabetical
835 order (Manipulation condition).

836 Fig. 3 General tendencies of theta power for Retention and Manipulation tasks (A) over the Left and
837 Right hemispheres and (B) in Anterior and Posterior areas. Error bars depict Standard Error of the Mean
838 (SEM).

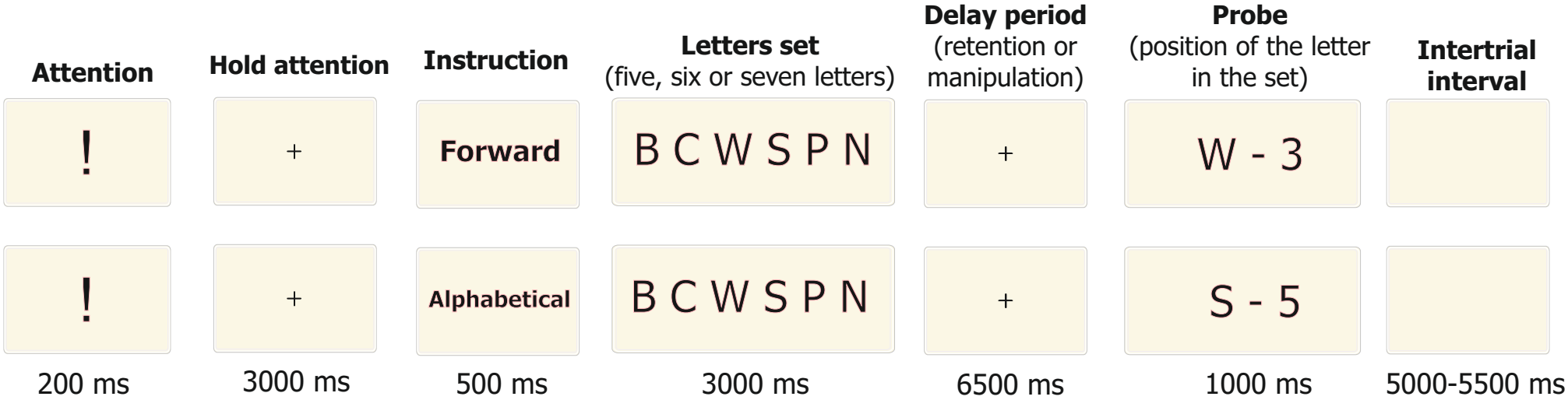
839 Fig. 4 Beta1 power chart and corresponding topograms for Retention and Manipulation tasks. Error bars
840 depict SEM.

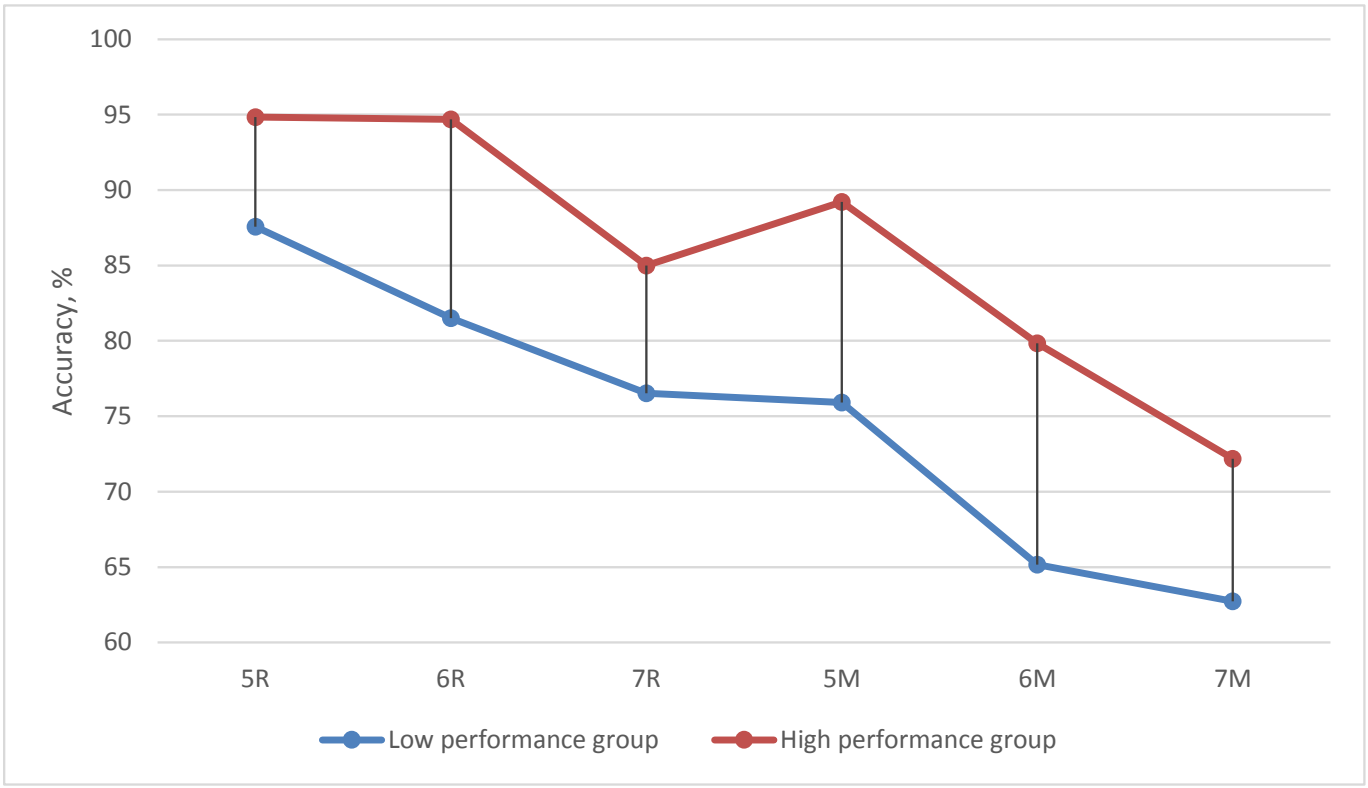
841 Fig. 5 (A) Midline theta power for four WM tasks and (B, C) corresponding topograms in two groups.
842 Notes: 5R, 7R – 5 and 7 letters Retention conditions; 5M, 7M –5 and 7 letters Manipulation conditions.
843 Error bars depict SEM.

844 Fig. 6 Alpha1 power for Retention and Manipulation tasks in Low and High performance groups. Error
845 bars depict SEM.

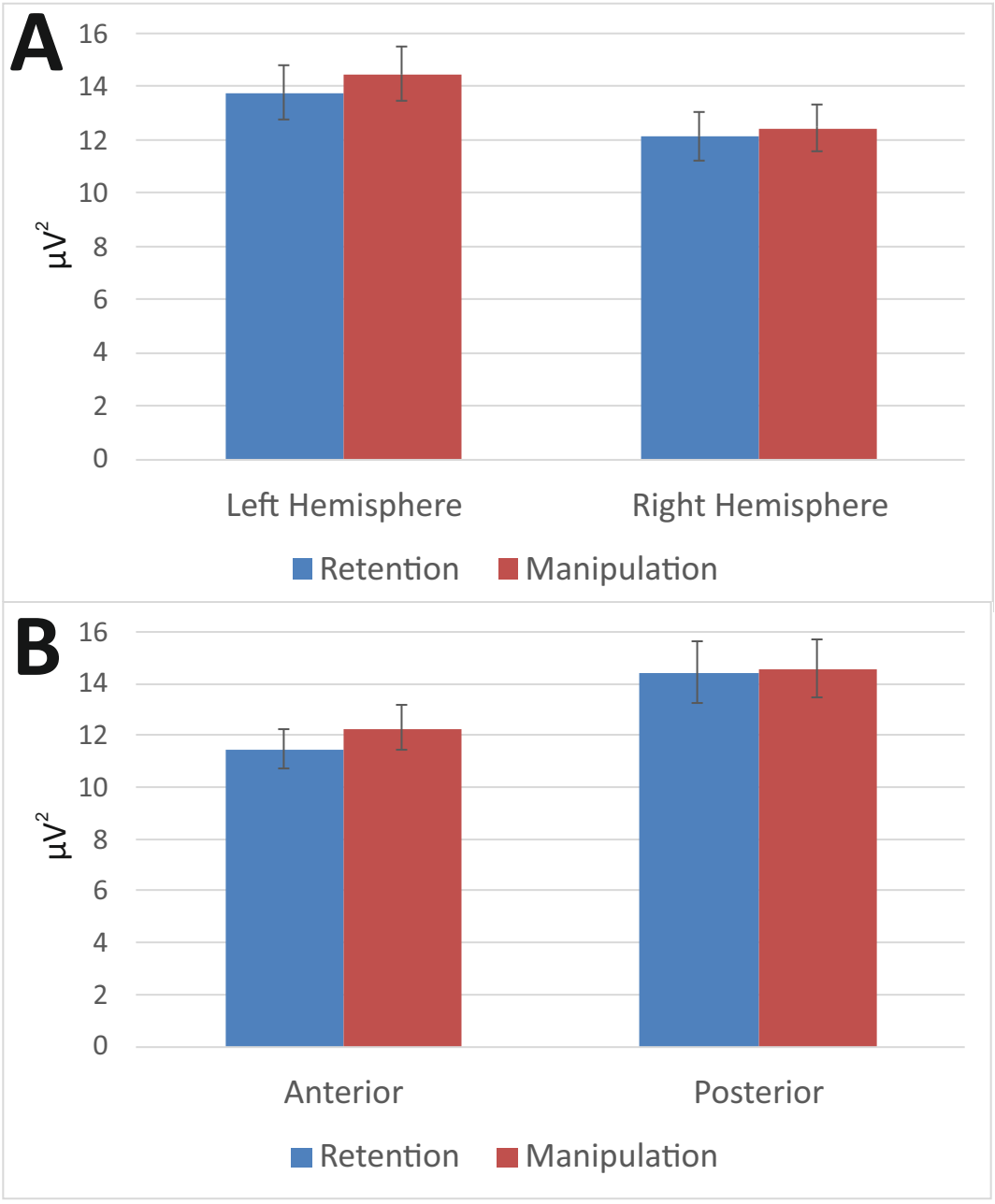
846 Fig. 7 (A) Beta1 power in the left posterior area for Retention and Manipulation tasks and corresponding
847 topograms (B) in Low performance (LP) and (C) High performance (HP) groups. Error bars depict SEM

848 Fig. 8 Beta2 power for Retention and Manipulation tasks in Low and High performance groups in
849 Anterior and Posterior areas. Error bars depict SEM.

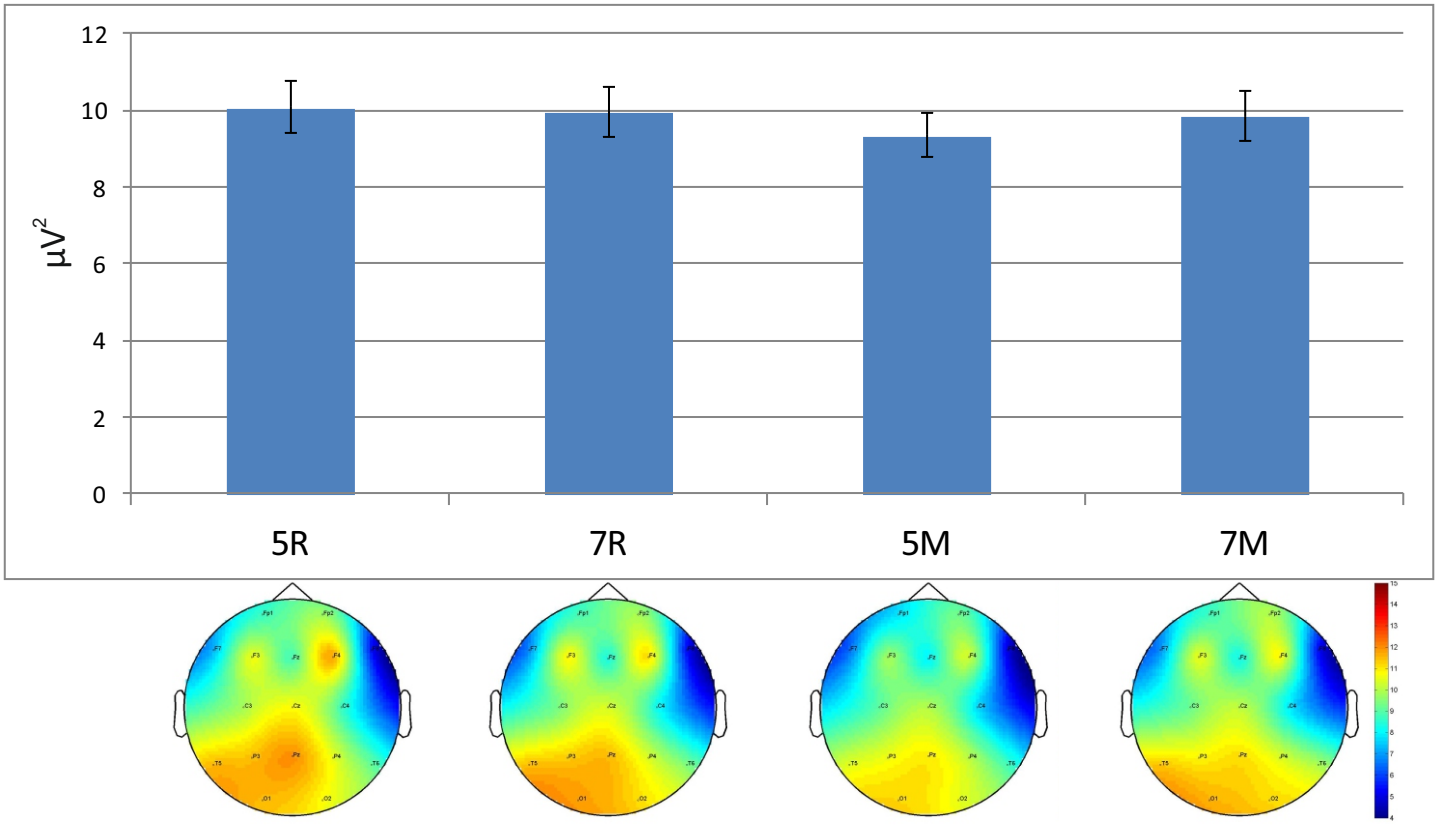

Attention
Hold attention
Instruction
Letters set
(five, six or seven letters)
Delay period
(retention or manipulation)
Probe
(position of the letter in the set)
Intertrial interval
!
+
Forward
B C W S P N
+
W - 3
!
+
Alphabetical
B C W S P N
+
S - 5
200 ms
3000 ms
500 ms
3000 ms
6500 ms
1000 ms
5000-5500 ms


100
95
90
85
80
75
70
65
60
Accuracy, %
5R
6R
7R
5M
6M
7M
Low performance group
High performance group

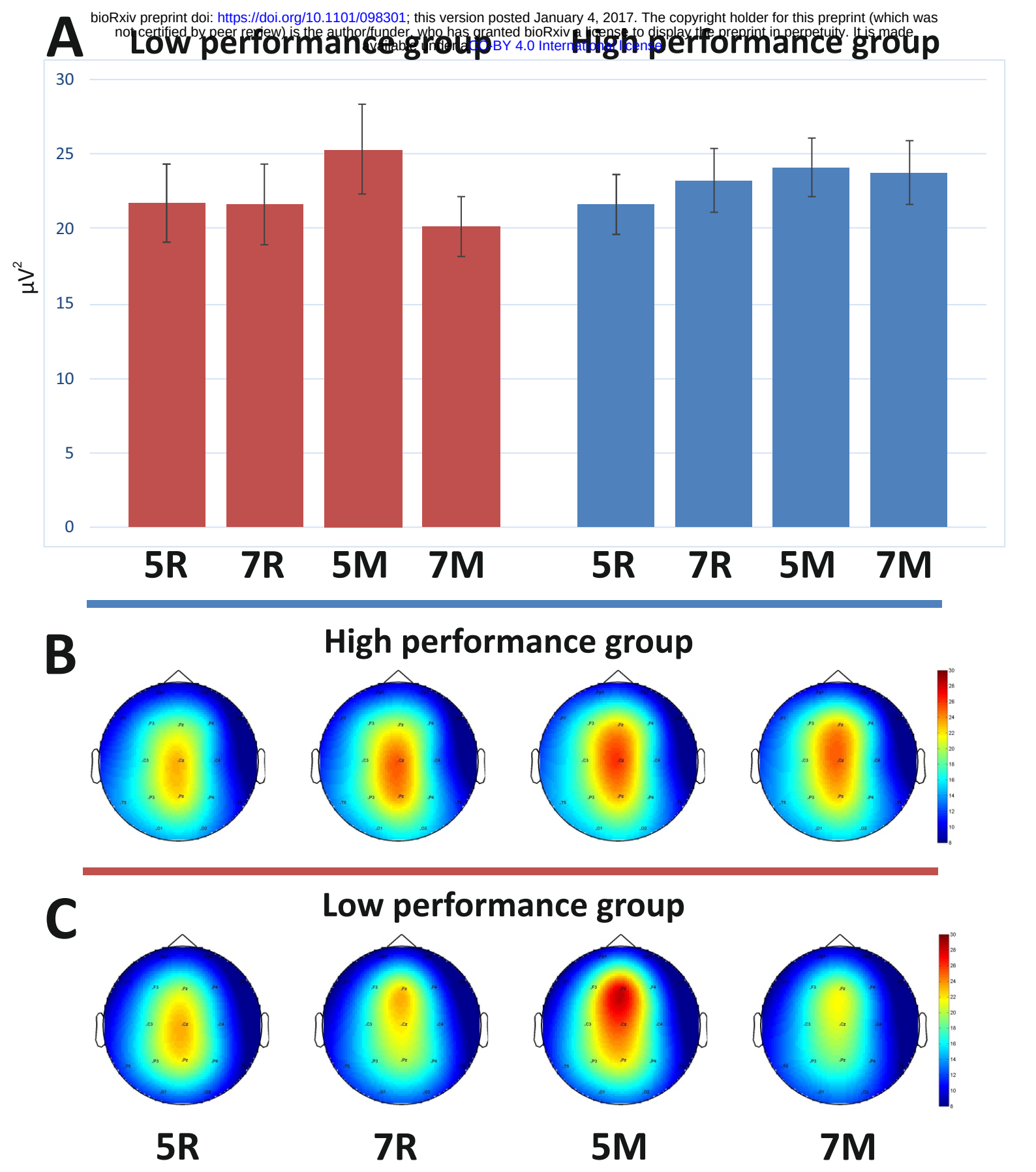
bioRxiv preprint doi: https://doi.org/10.1101/098301; this version posted January 4, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

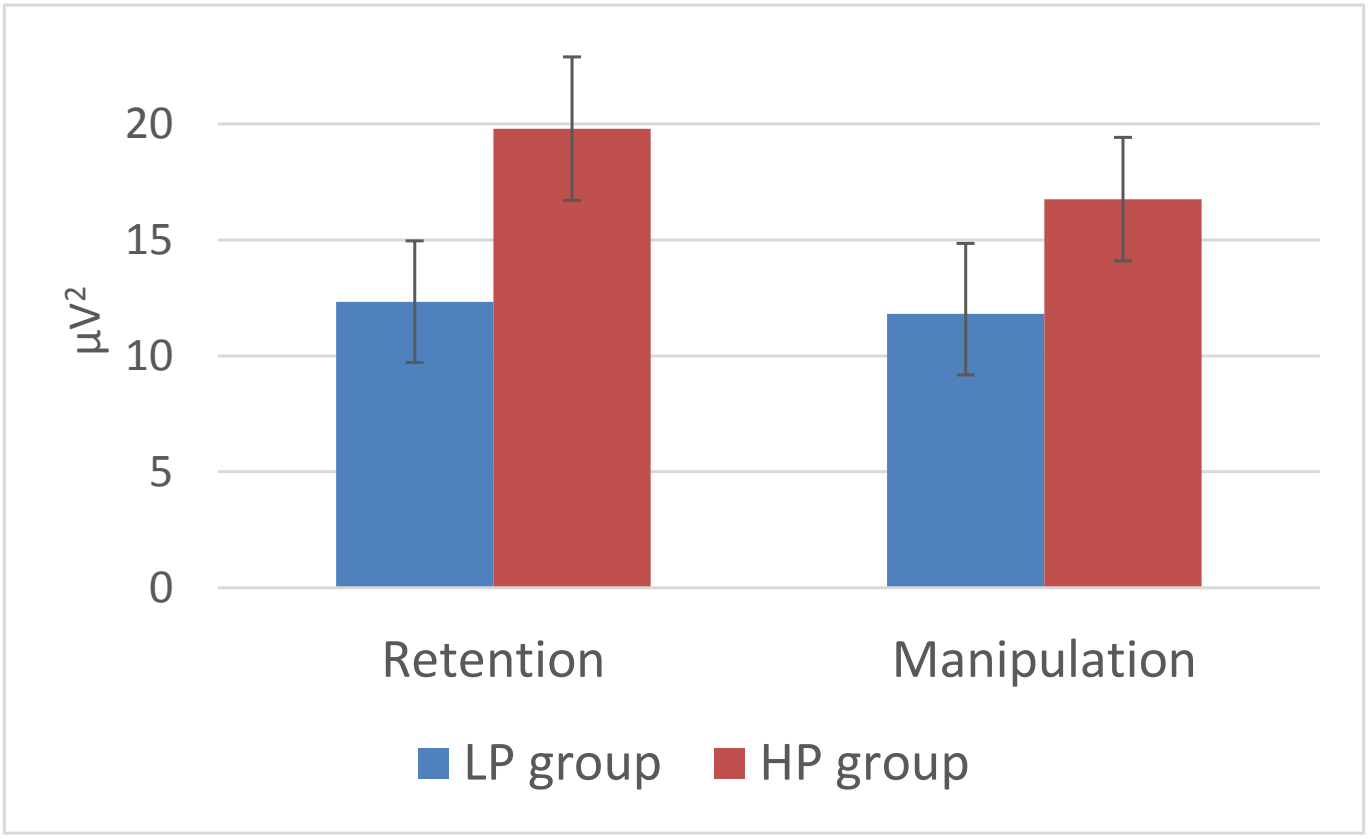


bioRxiv preprint doi: https://doi.org/10.1101/098301; this version posted January 4, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

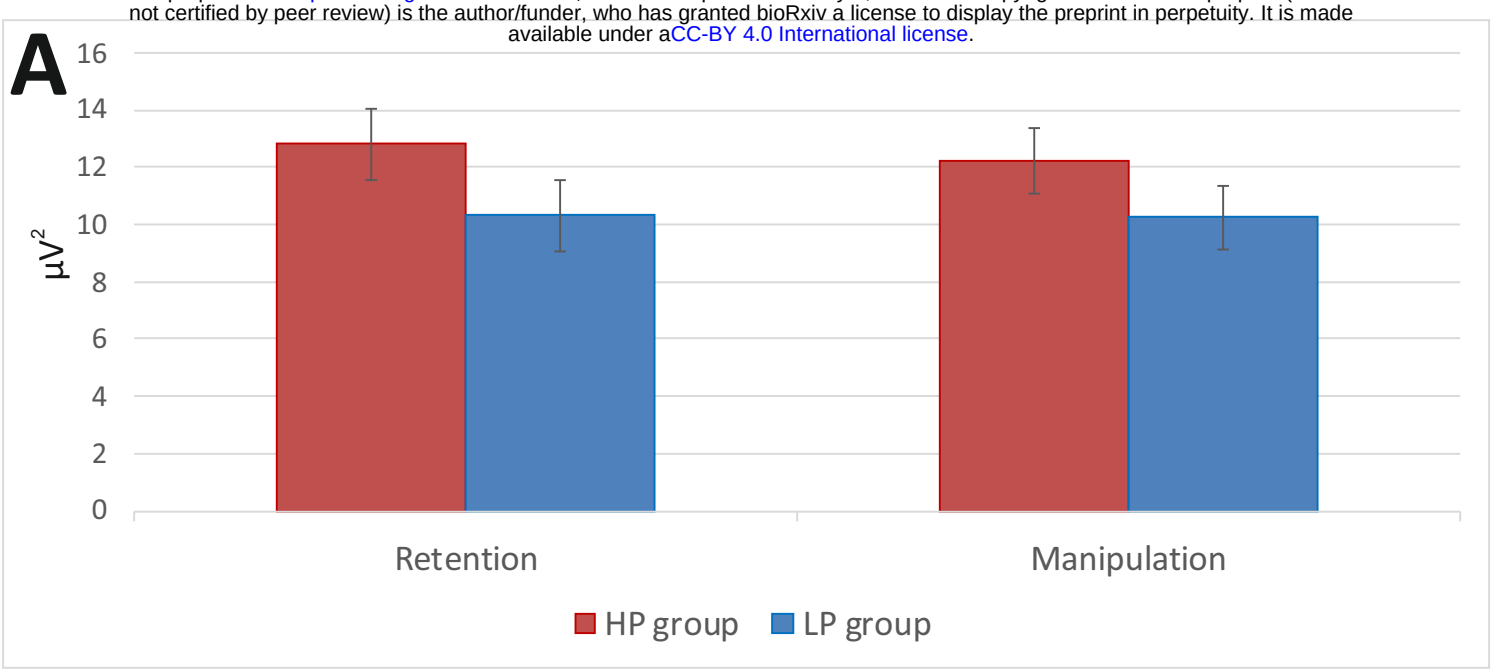


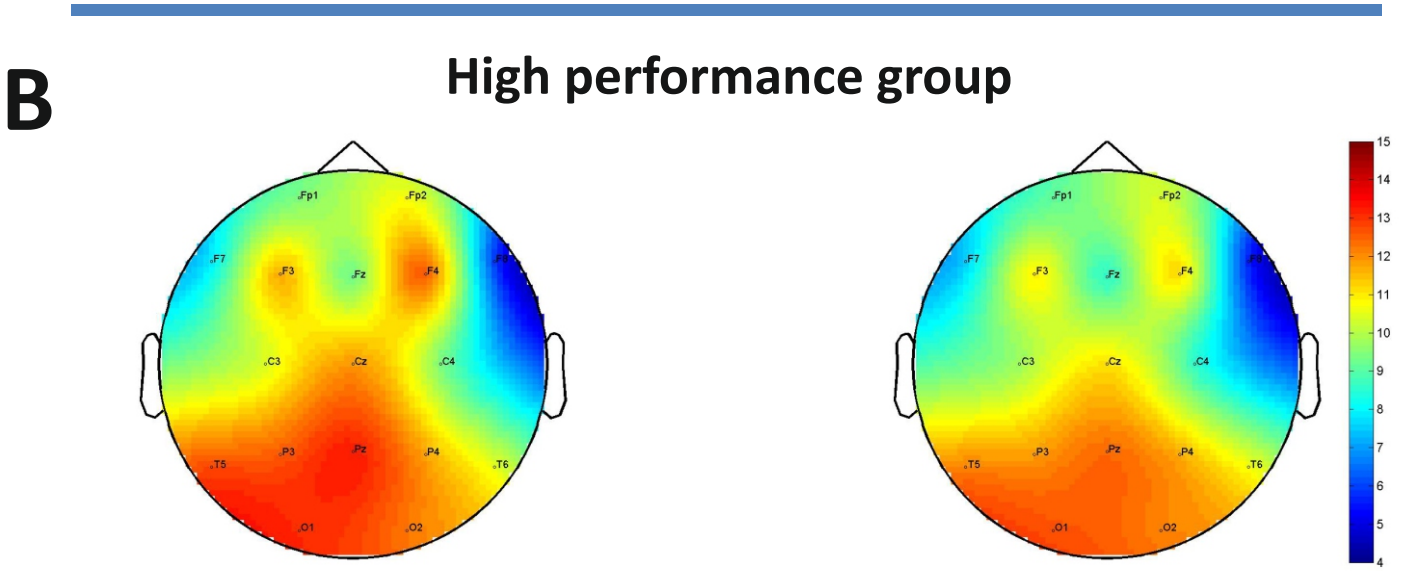
bioRxiv preprint doi: https://doi.org/10.1101/098301; this version posted January 4, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under a CC-BY 4.0 International license.

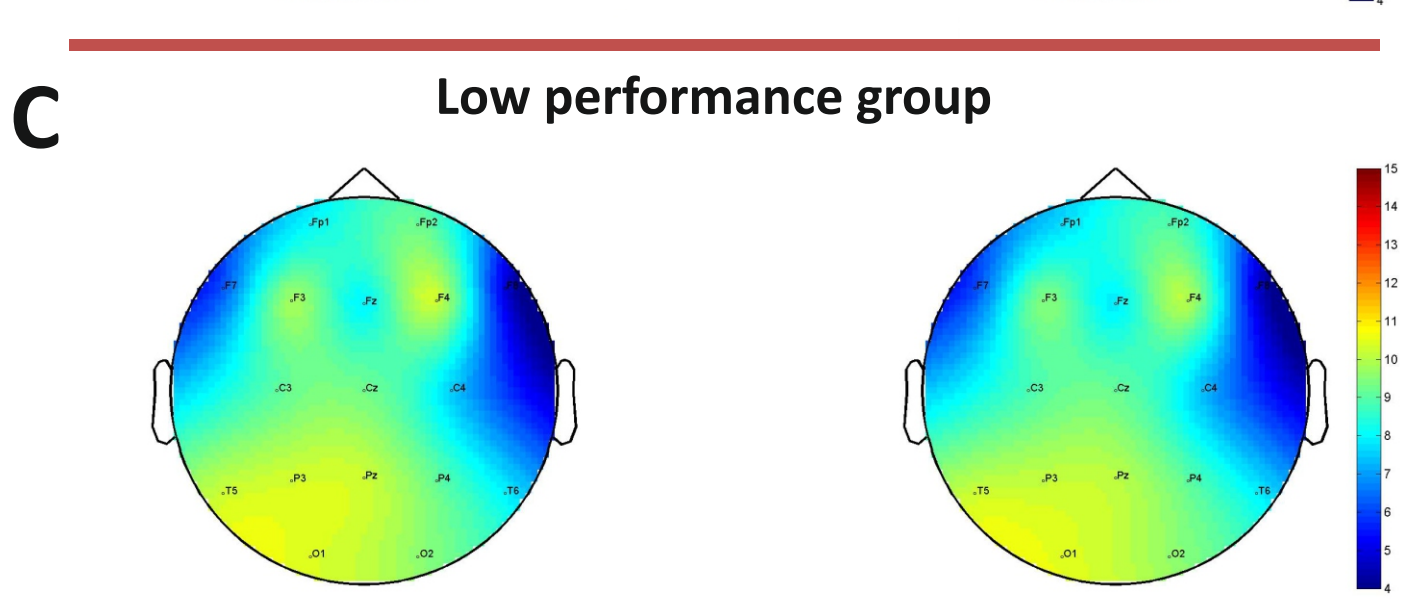


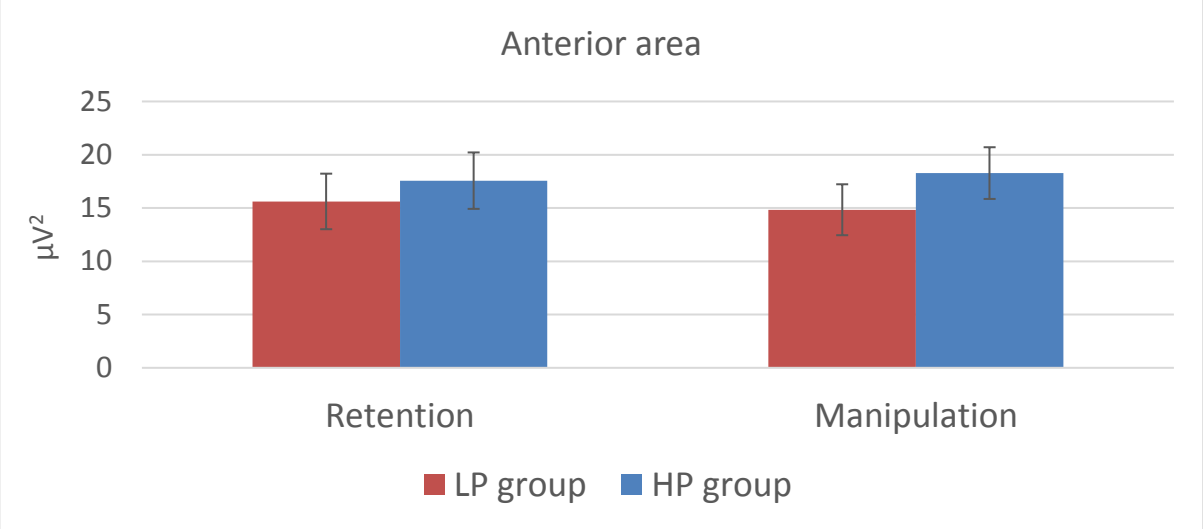

20
15
10
5
0
μV²
Retention
Manipulation
LP group
HP group

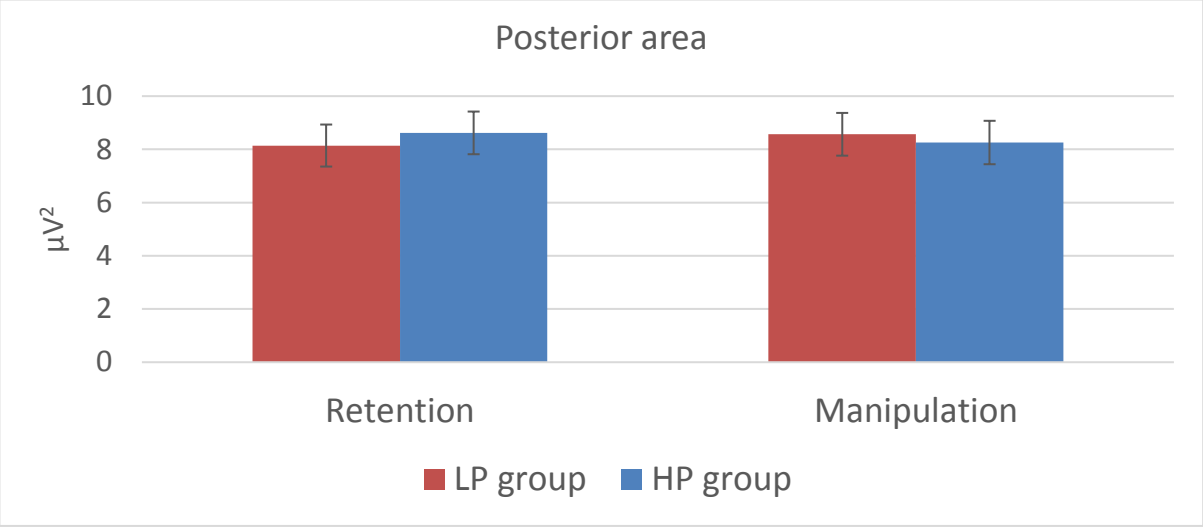
bioRxiv preprint doi: https://doi.org/10.1101/098301; this version posted January 4, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.








Anterior area
25
20
15
10
5
0
µV²
Retention
Manipulation
LP group
HP group


Posterior area
10
8
6
4
2
0
µV²
Retention
Manipulation
LP group
HP group