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The electrophysiological underpinnings of variation in verbal working memory capacity

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Working memory (WM) consists of short-term storage and executive components. We studied cortical oscillatory correlates of these two components in a large sample of 156 participants to assess separately the contribution of them to individual differences in WM. The participants were presented with WM tasks of above-average complexity. Some of the tasks required only storage in WM, others required storage and mental manipulations. Our data indicate a close relationship between frontal midline theta, central beta activity and the executive components of WM. The oscillatory counterparts of the executive components were associated with individual differences in verbal WM performance. In contrast, alpha activity was not related to the individual differences. The results demonstrate that executive components of WM, rather than short-term storage capacity, play the decisive role in individual WM capacity limits.

Working memory (WM)—our ability to maintain and manipulate information in a short term—is not a uniform construct. Although several theoretical models compete for the best explanation[1], most of them converge on the idea that WM entails (1) short-term storage for memory content (which can be regarded as a separate processing unit or as activated parts of long-term memory), and (2) executive components which are responsible for attentional control, protection from interference, active processing and reorganization, or manipulation of information in the short-term storage[2,3]. As regards the former, it should be distinguished from the ultrashort-term storage in iconic or echoic memory. As regards the latter, these executive components are what makes WM "working" and differentiates the WM in the proper sense from mere short-term memory. Most WM tasks in real life require both short-term storage and executive components. For example, keeping a phone number in mind until it is dialed requires transformation of verbal information into a sequence of button presses. The task also involves switching attention between the current number to dial and pressing buttons on the phone panel. A more complex example is the conversion of a shopping list into the optimal path while shopping. This task, in addition to the translation of the list into a sequence of spatial locations, also involves constant updating of information in WM.

Available electrophysiological data indicate that manipulation of information in WM is strongly related to theta oscillations (4–8 Hz) in the medial prefrontal and anterior cingulate cortex for manipulation of information in WM[4–12]. Therefore, theta is thought to reflect engagement of the executive components of WM[13]. In turn, posterior alpha activity (8–13 Hz) has been associated with short-term storage, and may directly underlie maintenance of information in WM[14,15]. Alpha activity responds to increasing load reaching an asymptote at the levels of individual's WM capacity[16]. Thus, posterior alpha activity can be seen as a reflection of the short-term storage component of WM.

The oscillatory mechanisms supporting individual WM capacity limits remain largely understudied. To study individual differences, large samples are essential. However, most available studies built their conclusions on samples of less than 30 individuals[16–25]. Better-powered studies (~ 35 participants per group) yielded mixed findings[11,26–28]. For instance, after a median split, only the high-performance group showed an increase of theta with load[11,28], suggesting that theta activity and the related executive functions are important for successful maintenance of WM. But another study did not find this relationship[27]. The relationship between alpha and beta activity and individual WM capacity is even less consistent.

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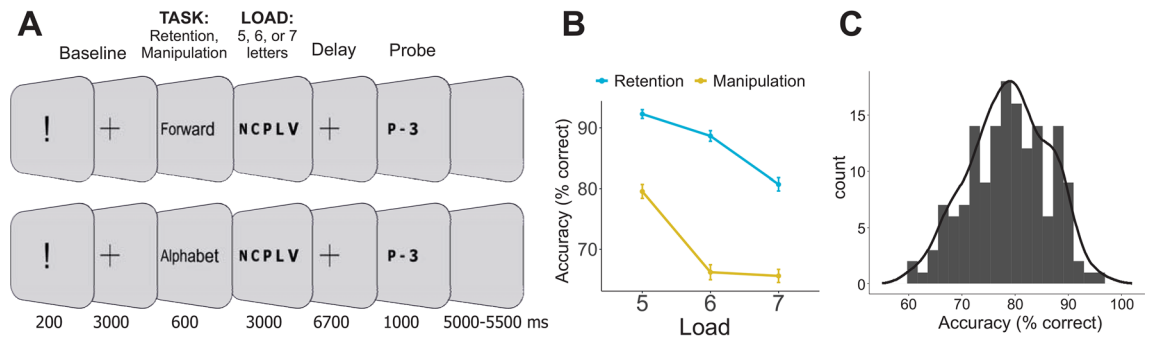
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Figure 1. (**A**) The experimental paradigm. (**B**) Average performance in 6 conditions. Error bars are standard errors of the mean. (**C**) Distribution of overall performance stacked into 25 bins.

The components of WM may contribute to individual differences in a different scale[29,30]. Here, we sought to provide solid data to set apart the contribution of oscillatory counterparts of short-term storage and executive components of WM to individual differences. To reach this goal, we analyzed EEG data from a large number of participants (N = 156) in WM tasks of above average complexity, which required either only retention of letter strings (Retention task) or retention and manipulation with the letters (mental recombination to the alphabetical order, Manipulation task) (see Fig. 1 for the experimental design). Increasing the complexity of the tasks allowed us to increase the variance, to avoid ceiling effect in performance and to better distinguish between low and high performers. The task with mental manipulations allowed us to assess the contribution of different WM components. Although even the simple retention of information involves executive components of WM, the executive load of retention is tangibly weaker than the load of mental manipulations with the same content. The manipulation task possesses all the properties that the retention task does but additionally, it involves executive components in a much larger extent. Thus, the differential score between the spectral power in the tasks allowed us to derive a neural index of executive components of WM – executive index. We hypothesized that (1) the power of alpha oscillations would be related to the capacity of the short-term storage component of WM, (2) the power of frontal midline theta would be related to the efficiency of the executive components of WM, and (3) the latter mechanism, but not the former one, would be related to the overall memory performance.

Results

Task performance. The accuracy was worse in the manipulation task and monotonically decreased with increasing WM load (main effect of Task: $F(1, 155) = 431.8$, $\eta^2 = 0.736$, $p < 0.001$; Load: $F(2, 307) = 138.8$, $\eta^2 = 0.472$, $p < 0.001$). The significant Task × Load interaction ($F(2, 305) = 22.1$, $\eta^2 = 0.125$, $p < 0.001$) resulted from the fact that load increment from 6 to 7 letters yielded a strong drop of accuracy in the retention task but no effect in the manipulation task (see Fig. 1B). All other pairwise differences were significant except the non-significant difference in performance between Retention of 7 and Manipulation of 5 letters.

Time–frequency analysis. We employed the linear mixed effects models (LME) to explore the relationship between behavioral performance (quantified as average accuracy across all conditions) and the spectral power in the theta frequency band. Although we used LME with a continuous Performance variable for statistical inference, for the ease of data interpretation and illustration purposes, the whole sample was median-split into the high performance (N = 78) and low performance (N = 78) groups on the basis of their average accuracy across all conditions.

As can be seen in Fig. 2, the high performance group exhibited a stronger theta increase in the Manipulation task than in the Retention task. This Task by Performance interaction (p = 0.004) resulted from the association between the relative theta power and behavioral performance being positive in the Manipulation task but negative in the Retention task (see Fig. 2 and Supplementary Table S1 for full statistical output).

Then, we correlated WM performance with the difference between theta in Manipulation and Retention tasks to test the hypothesis on the role of executive components of WM in individual differences. The larger was the difference between baseline normalized theta power in Manipulation and Retention conditions, the better the individual WM performance (Spearman's rho = 0.24, p = 0.002) (see Fig. 2C and Supplementary Figure S5 for full correlation matrix).

No significant main effect (p = 0.359) or interactions with Performance (Task x Performance: p = 0.454) were found in the alpha frequency band (see Fig. 3 and Supplementary Table S2).

Beta power negatively related to WM performance in the Manipulation task but not in the Retention task (Task by Performance interaction: p < 0.001; see Fig. 4 and Supplementary Table S3). Like it has been done with the theta activity, a subtraction of Retention beta from Manipulation beta was taken as an index of executive WM components. The correlation between this index and WM performance had similar magnitude as yielded in the analysis of theta (rho = − 0.26, p = 0.001), but with the opposite sign (see Fig. 4). Thus, better performance was related to lower beta activity.

Because the correlations of beta and theta executive indices with performance are similar, we tested whether the two represent the same underlying mechanism. The correlation between the constructs was in an expected direction but not statistically significant (rho = − 0.12, p = 0.124). Another way to test independence of the
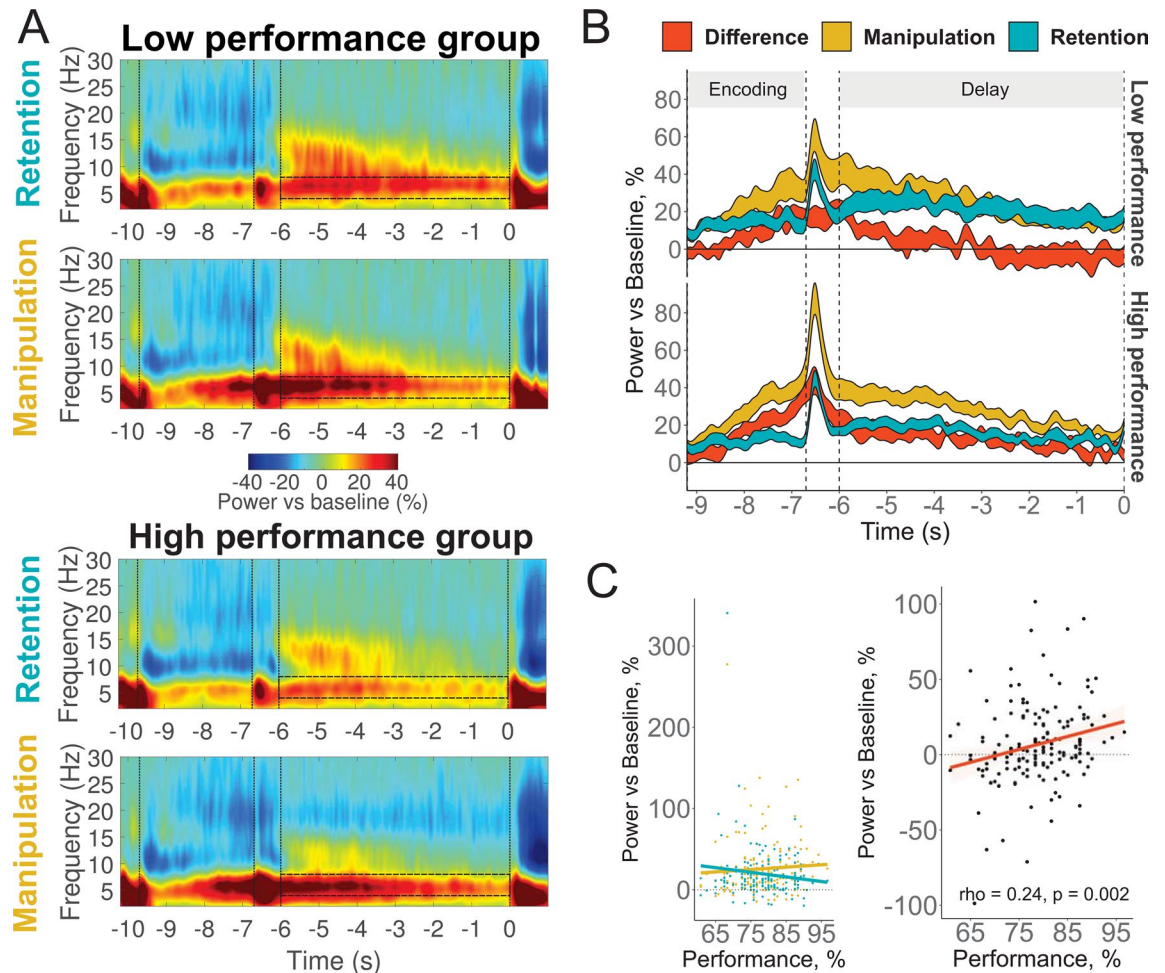
Figure 2. Relationship between theta power at Fz and WM performance. (**A**) Time–frequency maps in low (top panels) and high (bottom panels) performance groups in retention and manipulation tasks. Semi-transparent boxes mark time–frequency windows of interest (4–8 Hz, last 6 s of the delay). The first vertical bar marks the onset of encoding; the second one marks the onset of the delay; the third one marks the beginning of the time–frequency window of interest; and the fourth one marks the onset of retrieval. (**B**) The time dynamics of theta activity in Retention, Manipulation tasks and their difference: the result of subtraction of theta relative power in the retention task from the power in the manipulation task (executive index). The width of the line represents 2 standard errors of the mean. (**C**) Left panel: correlation of WM performance in the manipulation and retention tasks. Right panel: correlation of WM performance and the executive index. Performance is the average percent accuracy in all conditions.

executive indices is to use Bayesian linear regression. Employing this approach, we, first, compared all three possible models—only difference score beta, only difference score theta, and a combination of both difference scores as IVs—with the intercept only model. Second, we compared the one predictor models with the two predictors model. The model preferred by Bayes factor is the two predictors model (BF = 135.48), and the model is 14.61 times better than only theta (BF = 9.27), and 3.85 times better than only beta model (BF = 35.23). The fact that the highest Bayes factor was yielded by the two predictors model suggests that their contribution is largely independent. Thus, theta and beta may play independent roles in individual differences in WM.

To check the reliability of the above effects we used a residual change score instead of difference as difference scores. Using a residual change scores for theta (rho = 0.24, p = 0.003) and beta (rho = − 0.28, p < 0.001) successfully replicated the results obtained with the difference scores. The correlation between alpha and performance remained non-significant (rho = − 0.06, p = 0.49).

Discussion

We found that two EEG indices of the executive components of WM (calculated as the difference between the relative spectral power in the retention and the manipulation conditions or, alternatively, as residual change scores) significantly correlated with WM performance in a large sample of healthy individuals. These findings confirm our hypothesis (iii) stating that oscillatory associates of the executive WM components, but not of the storage component, are related to WM performance. This is congruent with previous behavioral research indicating that individual differences in executive functions were better predictors of WM capacity than differences in short-term storage[30,32,33].
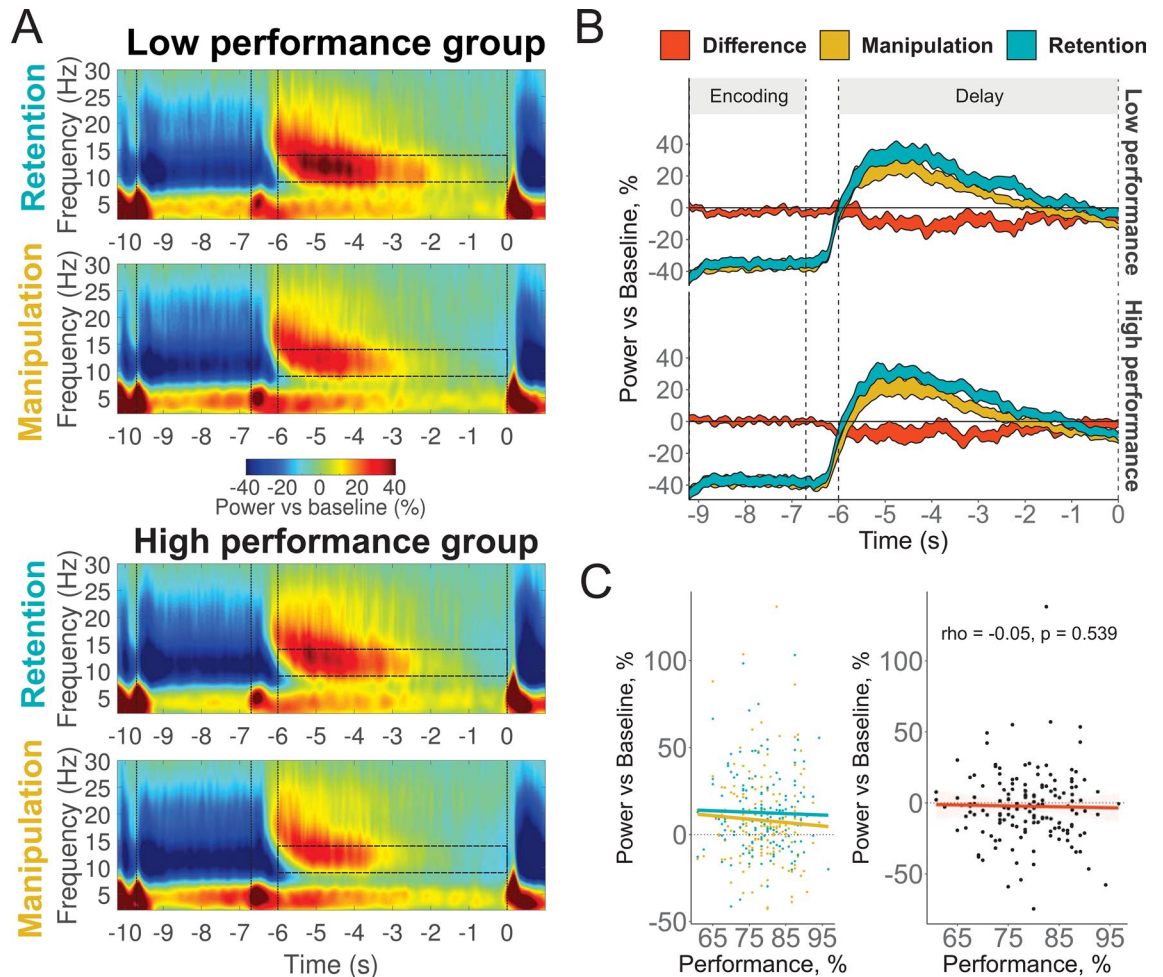
Figure 3. Relationship between alpha power over posterior ROI (P3, T5, O1, P4, T6, O2) and WM performance. (**A**) Time–frequency maps in low (top panels) and high (bottom panels) performance groups in retention and manipulation tasks. Semi-transparent boxes mark time–frequency windows of interest (9–14 Hz, last 6 s of the delay). The first vertical bar marks the onset of encoding; the second one marks the onset of the delay; the third one marks the beginning of the time–frequency window of interest; and the fourth one marks the onset of retrieval. (**B**) The time dynamics of alpha activity in Retention, Manipulation tasks and their difference: the result of subtraction of alpha relative power in the retention task from the power in the manipulation task (executive index). The width of the line represents 2 standard errors of the mean. (**C**) Left panel: correlation of WM performance in the manipulation and retention tasks. Right panel: correlation of WM performance and the executive index. Performance is the average percent accuracy in all conditions.

The positive correlation between WM performance and the theta executive index, (i.e., more theta, better performance) also confirms our hypothesis (ii). Although in STM tasks the demand on executive functions is considerably lower than in genuine WM tasks, it is not completely lacking. For example, when WM load is high, executive components of WM are needed to counteract interference and to suppress irrelevant information. Few studies demonstrated a correlation between theta activity and performance in verbal (Zakrzewska & Brzezicka[28]: N = 69, r = 0.32, Kwon et al.[21]: N = 13, r = 0.76) and visual (Kawasaki & Yamaguchi[20]: N = 14, r = 0.51; Maurer et al.[22]: N = 24, r = − 0.41) short-term memory tasks that require only retention of, but no manipulation with, stimulus material. In contrast, we found no correlation between theta activity in the retention task and behavioral performance (rho = − 0.01, p = 0.88). Due to the known effects of saturation of brain activity measures with reaching higher levels of load[16,34–36], we hypothesized that the role of theta in retention tasks may be limited to only lower levels of load. However, even at the lowest level of 5 letters the correlation between theta during retention and the accuracy was not significant (rho = − 0.03, p = 0.67). Thus, theta increase during delay in simple tasks was not predictive in genuine WM tasks.

Contrary to theta, the beta index of the executive control negatively correlated with WM performance (i.e., more beta, worse performance). This finding was not predicted by any hypothesis because the literature concerning this relationship is too scarce. Probably the only comparable study is a spatial WM MEG experiment[37,38]. Both publications reported a negative correlation between beta (15–20 Hz) and behavioral performance. Although the two reports shared the same sample, the localization of the correlation was different: WM performance correlated with beta activity in the right superior parietal lobule in one paper, and in the left dorsolateral prefrontal
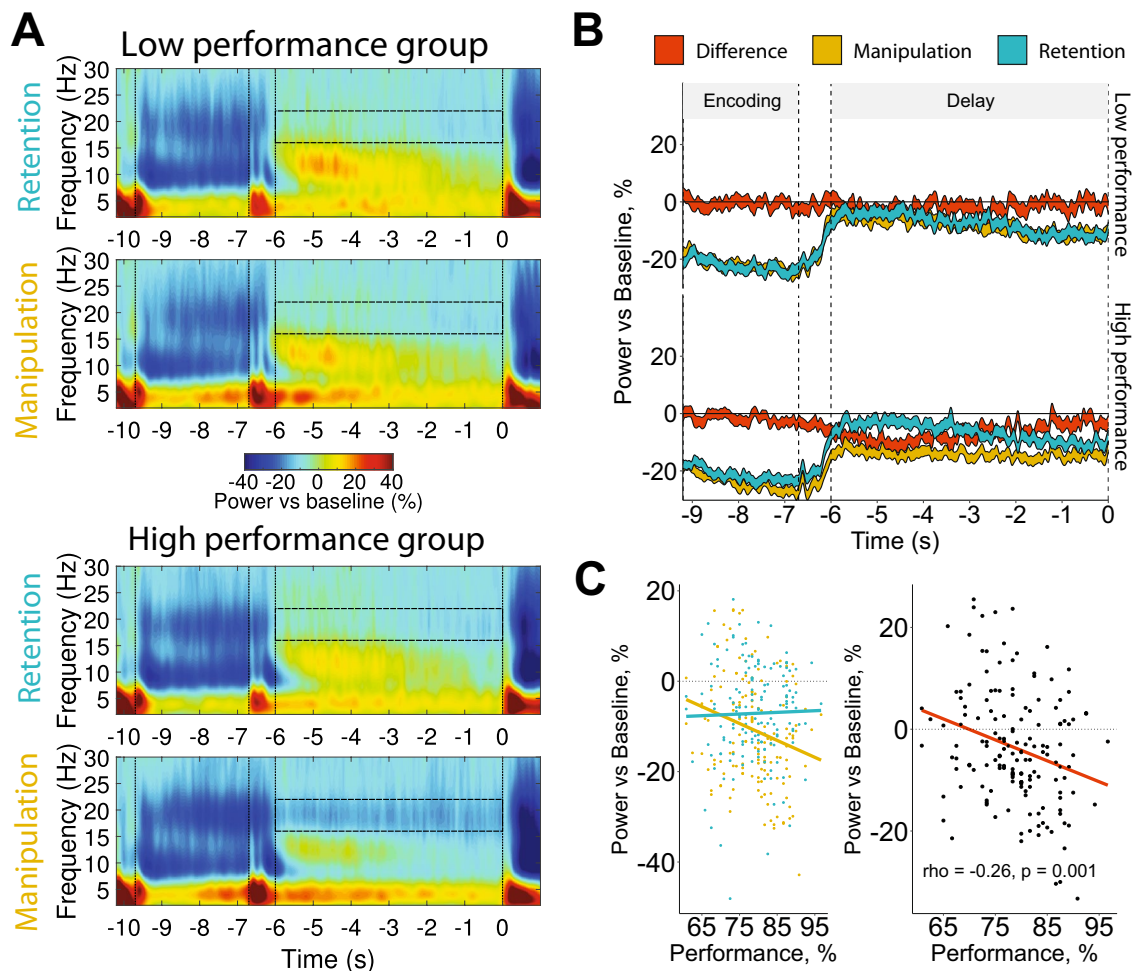
Figure 4. Relationship between beta power over central ROI (Cz, C4, C3) and WM performance. (**A**) Time–frequency maps in low (top panels) and high (bottom panels) performance groups in retention and manipulation tasks. Semi-transparent boxes mark time–frequency windows of interest (16–22 Hz, last 6 s of the delay). The first vertical bar marks the onset of encoding; the second one marks the onset of the delay; the third one marks the beginning of the time–frequency window of interest; and the fourth one marks the onset of retrieval. (**B**) The time dynamics of beta activity in Retention, Manipulation tasks and their difference: the result of subtraction of beta relative power in the retention task from the power in the manipulation task (executive index). The width of the line represents 2 standard errors of the mean. (**C**) Left panel: correlation of WM performance in the manipulation and retention tasks. Right panel: correlation of WM performance and the executive index. Performance is the average percent accuracy in all conditions.

cortex and the bilateral superior temporal gyrus in the other. Moreover, beta activity in the two reports correlated with two different indexes of WM performance. These inconsistencies cast doubt on the reliability of the results.

Beta desynchronization may reflect switching internal attention between the reorganized set of letters and the initial set during the manipulations. Even when attention shifts from one object to another occur without eye movements, the shifts activate the same cortical areas as real eye movements[39]. A good example is the activation of frontal eye fields (FEF) found in a spatial manipulation task[40]. If the beta activity observed in our study is related to activation of motor control networks, then why was it related to individual differences in WM? Repetitive saccade eye movements during delay were shown to increase episodic memory performance[41,42]. The movements executed just before blocks of an attentional control task (Flanker) also improved performance in the task[43]. The attentional enhancement by preactivation of fronto-parietal network nodes such as FEF was hypothesized to produce the above mentioned effects[43]. Consistent with this idea, TMS delivered to FEF improved detection of targets in a visuospatial attention task[39], whereas a suppression of the same region by TMS decreased inhibitory control[44]. It is admittedly a speculation at this point, but more efficient use of FEF to execute mental manipulations would potentially facilitate WM performance in our study.

Our hypothesis (i) predicted a significant link between alpha activity and the short-term storage capacity. This hypothesis was not confirmed. Although this link can be expected on the basis of theoretical considerations (as mentioned above in the Introduction), empirical data are not very consistent. Correlations between WM capacity and posterior alpha can be strongly negative (Kawasaki & Yamaguchi[20]: visual WM, N = 14, r = 0.66) or strongly positive (Kwon et al.[21]: verbal WM, N = 13, r = 0.75). Another study found no correlation between WM

performance and relative alpha power in the Sternberg task (Sghirripa et al.[25]; N = 24). Better WM performance was associated, in some studies, with stronger alpha enhancement in more difficult tasks than in the easy tasks (Hu et al.[19]: N = 20, r = 0.55; N = 23, r = 0.59), in other studies, however, with stronger alpha suppression in more difficult tasks (Erickson et al.[26]: N = 60, r = 0.45; Fukuda et al.[16]: N = 28, r = 0.48). In a yet another study the positive correlation between the WM capacity and alpha modulation from lower to the higher load did not reach significance (Roux et al.[24]: N = 25, r = 0.39). We calculated the alpha modulation index (within-subject linear regression coefficients of alpha power by Load), as used in the verbal WM study by Hu et al.[19]. The test attained significance neither for the overall task performance (rho = 0.04, p = 0.64), nor for the retention task only (rho = 0.03, p = 0.72).

Therefore, not all correlations obtained in the previous studies were replicated in a larger sample. One might suggest that our negative result is due to using only high-load conditions, and that stronger correlations would be obtained if we compared alpha between high-load and low-load conditions. Nevertheless, the individuals with higher WM capacity did not show signs of larger short-term storage that would have been reflected in the modulation of alpha at the high levels of load. We suggest that instead it is the executive control as reflected in the theta activity that controls attention and minimizes the interference, thus determining an individual's WM capacity.

The interference hypothesis of WM capacity assumes that WM is affected not only by external distractors but also by mutual interference between the items[45–47]. Thus, the detrimental effect on memory precision is a function of the number of items stored in WM and the presence of the concurrent task. When WM load is high and/ or manipulations are required, the executive component of WM is needed to cope with interference. Perhaps, the resources that can be deployed to counteract interference are better represented in the higher performing individuals.

There is another possible mechanism to explain how executive processes may cope with increasing WM demands. Camos & Barrouillet[48] suggested that attention is involved in rapid refreshment of memory traces, thus preventing temporal decay of the WM content. The non-refreshed information fades out and in the worst case cannot be recovered. In extension of this model, beta and theta activity reflect the ability to maintain information in the active state by switching the focus of attention between items, thus defining the individual capacity limit.

Above we interpreted changes in posterior alpha rhythm as a reflection of the demand on the short-term storage component of WM. Another interpretation regards alpha as a mechanism of filtering information by gating only relevant sensory stimuli[49,50]. If we accept this view, then either higher WM capacity individuals are no more efficient in the filtering out task-irrelevant information than lower WM capacity individuals, or the alpha filtering mechanism works only under moderate levels of memory load.

To summarize, our data indicate a close relationship between medial frontal theta, central beta activity, and the executive components of WM. Both oscillatory indices of executive processes, manifested in the theta (as we expected) and beta (unexpectedly) frequency bands, were related to behavioral performance in a verbal WM task. In contrast, we could not replicate the data indicating the important role of posterior alpha in WM performance. We can conclude that the ability to control attention plays a larger role in individual differences in WM than the capacity of the short-term storage.

Methods

Participants.   186 individuals participated initially in the study. Eight participants with overall performance below 60% were excluded. Furthermore, a subsequent analysis revealed 22 EEG records with an excessive number of artefacts (less than 12 clean trials in any condition). Thus, 156 participants (82 females, mean age = 21.23, SD = 3.22) were included in the final sample. The participants had normal or corrected-to-normal vision and self-reported no history of neurological or mental diseases. All the participants were Russian native speakers. The experimental protocol was approved by the Ural Federal University ethics committee, and conducted in accordance with the Declaration of Helsinki. Informed consent was obtained from all participants.

Stimuli.   Sets of Cyrillic alphabet letters written in capitals were used as stimuli. All letters (vowels and consonants) had been selected randomly from the alphabet, had random order, and no repetitions in the sets. The pool of stimuli comprised 1200 sets of letters (400 per level of load) which were manually checked to not form any meaningful words. An analogue using Latin letters and English words is shown in Fig. 1.

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 on the cross whenever it appeared. Next, the word "forward" or "alphabetical", presented for 600 ms, instructed the participants whether they would have to maintain in memory the original set as it was presented (retention task) or, first, mentally reorganize the letters into the alphabetical order and then maintain the result in memory (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 6700 ms. At the end of the 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 probe was presented for 1000 ms. Depending on the task, the participants indicated whether the probe was on the corresponding position either in the original set (retention task), or in the set resulted from alphabetical reordering (manipulation task). The participants were asked to press one of the computer mouse buttons (left or right) if the probe was correct and the other button otherwise. The two buttons were attributed to the 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 randomized. The next trial started after a blank interval that varied between 5000 and 5500 ms.

The experiment entailed six different conditions: maintenance in memory of 5, 6 or 7 letters in the alphabetical (manipulation condition) or forward (retention condition) order. Each condition had 20 consecutive trials. These six blocks of 20 trials were presented in a random order. Two practice blocks with 3 and 6 trials respectively were given shortly before the main experiment.

During the experiment, the participants were seated in a comfortable armchair in front of a computer 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°.

EEG recording and preprocessing.   The EEG was recorded from 19 electrodes arranged according to the 10–20 system using Mitsar-EEG-202 amplifier with averaged earlobes reference. Two additional electrodes were used for horizontal and vertical EOG. EEG data were acquired with 500 Hz sampling rate and 150 Hz low-pass filter.

The procedure of EEG artifacts suppression and removal was conducted in two steps. At the first step, in order to suppress ocular activity artifacts, the independent component analysis (ICA) was performed using AMICA algorithm[51]. The components clearly related to blinks and eye movements were identified and removed after visual exploration of the data. At the second step, epochs still containing artefacts were visually identified and discarded.

EEGLAB toolbox[52] for MATLAB was used for the data preprocessing.

Time–frequency analysis.   Before the time–frequency analysis, 1 Hz high-pass, 45 Hz low-pass and 50 Hz notch filters were applied with the EEGLAB firfilt function. Then, epochs in [− 14,200 2200 ms] interval where 0 is the onset of the probe were created.

The EEG time series in each epoch were convolved with a set of complex Morlet wavelets. The wavelets were defined as the product of a complex sine wave and a Gaussian window – $e^{-i2\pi tf} e^{-t^2/(2\sigma^2)}$, where t is time, f is frequency. σ is the width of the Gaussian, which set according to $n/(2\pi f)$, where n is the number of cycles – the parameter defining the time–frequency precision trade-off. The frequency f increased from 1 to 45 Hz in 45 linearly spaced steps, and the number of cycles n increased from 3 to 12 in 45 logarithmically spaced steps. From the resulting complex signal, the power of each frequency at each time point was obtained. The power was baseline-normalized by computing the percent change of the power in respect to [− 11,500 − 10,500] ms interval (i.e. "Baseline" in Fig. 1).

The time–frequency analysis was performed by means of the Fieldtrip toolbox[53].

Statistics.   In order to decrease the number of factors employed in statistical calculations we defined frequency-channels regions of interest (ROI) with maximal representation of certain frequencies in certain group of channels. Thus, theta (4–8 Hz) had the maximal power at Fz, alpha (9–14 Hz) at posterior channels (left: T5, P3, O1; right: T6, P4, O2) and beta (16–22 Hz) at central channels (C3, Cz, C4) (see Supplementary materials for time–frequency maps at each channel).

Then spectral power was averaged in the ROIs in a 6 s time interval corresponding to the delay period (see Fig. 2). We excluded the initial 700 ms from the onset of Delay period. As can be seen in Fig. 2 and Supplementary Fig. 1, the first few hundred milliseconds after the onset of the delay contain evoked response activity that could distort the frequency data if not rejected[54–56].

For statistical analysis of behavioral data, we employed repeated-measures analysis of variance (RM ANOVA) with factors Task (2 levels: Manipulation, Retention) and Load (3 levels: 5, 6, 7 letters to memorize).

For EEG data analyses we employed linear mixed-effects models (LME). As recommended by Barr et al.[57], first, we always tried to fit the maximal model. In the case of the convergence problem, we first tried to fit the model with main effect random slopes (no interactions). If it converged, next, we again followed the advice by Barr[58] and reduced the maximal random effect structure keeping the highest-order interaction slope (e.g., Task x Load x Hemisphere for alpha rhythm) and slopes that showed significant interactions with Performance at the previous step. Before fitting the models, continuous independent variables were centered around zero, and qualitative variables were effect coded.

For beta and theta rhythms the maximal model included Task and Load, Performance and all possible interactions as fixed effects, Participant as a grouping random intercept effect, and combination of Task, Load and their interactions as random slopes. For alpha activity fixed and random effects of Hemisphere (2 levels: left, right) were additionally included, because alpha frequently shows an asymmetry during delay period[59]. Performance was calculated as the mean percentage of correct answers averaged over all conditions. In this case Performance plays the role of a personal trait and allows a straightforward interpretation of possible interactions with the other fixed effects. Single trial EEG data entered the analysis.

lme4 package[60] and function lmer in *R* was used to fit the models. For the calculation of p-values we used lmerTest package[61] with the default Satterthwaite's degrees of freedom approximation.

We decided to use the alpha level of 0.005, as such a threshold exhibits higher evidential value and may also help to improve reproducibility of newly discovered effects (e.g. see Benjamin et al.[62] but also Miller & Ulrich [63] for another opinion).

Reliability estimates (Cronbach's alpha) for behavioral and EEG variables in the manipulation and retention tasks are reported in Supplementary Table S4.

All statistical calculations were performed in *R,* version 3.6.3[64].

Data availability

The datasets generated and/or analyzed during the current study are available from the corresponding author on request, without undue reservation.

References

1. Miyake, A. & Shah, P. *Models of Working Memory: Mechanisms of Active Maintenance and Executive Control.* (Cambridge University Press, Cambridge, 1999).
2. Baddeley, A. Working memory: theories, models, and controversies. *Annu. Rev. Psychol.* **63**, 1–29 (2012).
3. Engle, R. W. & Kane, M. J. Executive attention, working memory capacity, and a two-factor theory of cognitive control. *Psychol. Learn. Motiv.* **44**, 145–200 (2004).
4. Berger, B. *et al.* Dynamic regulation of interregional cortical communication by slow brain oscillations during working memory. *Nat. Commun.* **10**, 1–11 (2019).
5. Berger, B., Omer, S., Minarik, T., Sterr, A. & Sauseng, P. Interacting memory Systems—Does EEG alpha activity respond to semantic long-term memory access in a working memory task?. *Biology* **4**, 1–16 (2014).
6. Eschmann, K. C. J., Bader, R. & Mecklinger, A. Topographical differences of frontal-midline theta activity reflect functional differences in cognitive control abilities. *Brain Cogn.* **123**, 57–64 (2018).
7. Griesmayr, B., Gruber, W. R., Klimesch, W. & Sauseng, P. Human frontal midline theta and its synchronization to gamma during a verbal delayed match to sample task. *Neurobiol. Learn. Mem.* **93**, 208–215 (2010).
8. Itthipuripat, S., Wessel, J. R. & Aron, A. R. Frontal theta is a signature of successful working memory manipulation. *Exp. Brain Res.* **224**, 255–262 (2013).
9. Kawasaki, M., Kitajo, K. & Yamaguchi, Y. Dynamic links between theta executive functions and alpha storage buffers in auditory and visual working memory. *Eur. J. Neurosci.* **31**, 1683–1689 (2010).
10. Kawasaki, M. & Watanabe, M. Oscillatory gamma and theta activity during repeated mental manipulations of a visual image. *Neurosci. Lett.* **422**, 141–145 (2007).
11. Pavlov, Y. G. & Kotchoubey, B. EEG correlates of working memory performance in females. *BMC Neurosci.* **18**, 26 (2017).
12. Sauseng, P. *et al.* EEG alpha synchronization and functional coupling during top-down processing in a working memory task. *Hum. Brain Mapp.* **26**, 148–155 (2005).
13. Sauseng, P., Griesmayr, B., Freunberger, R. & Klimesch, W. Control mechanisms in working memory: a possible function of EEG theta oscillations. *Neurosci. Biobehav. Rev.* **34**, 1015–1022 (2010).
14. Roux, F. & Uhlhaas, P. J. Working memory and neural oscillations: alpha-gamma versus theta-gamma codes for distinct WM information?. *Trends Cogn. Sci.* **18**, 16–25 (2014).
15. van Ede, F. Mnemonic and attentional roles for states of attenuated alpha oscillations in perceptual working memory: a review. *Eur. J. Neurosci.* **48**, 2509–2515 (2018).
16. Fukuda, K., Mance, I. & Vogel, E. K. Alpha power modulation and event-related slow wave provide dissociable correlates of visual working memory. *J. Neurosci.* **35**, 14009–14016 (2015).
17. Bashivan, P., Bidelman, G. M. & Yeasin, M. Spectrotemporal dynamics of the EEG during working memory encoding and maintenance predicts individual behavioral capacity. *Eur. J. Neurosci.* **40**, 3774–3784 (2014).
18. Hsieh, L. T., Ekstrom, A. D. & Ranganath, C. Neural oscillations associated with item and temporal order maintenance in working memory. *J. Neurosci.* **31**, 10803–10810 (2011).
19. Hu, Z. *et al.* Working memory capacity is negatively associated with memory load modulation of alpha oscillations in retention of verbal working memory. *J. Cogn. Neurosci.* (2019) https://doi.org/10.1162/jocn_a_01461.
20. Kawasaki, M. & Yamaguchi, Y. Frontal theta and beta synchronizations for monetary reward increase visual working memory capacity. *Soc. Cogn. Affect. Neurosci.* **8**, 523–530 (2013).
21. Kwon, G. *et al.* Individual differences in oscillatory brain activity in response to varying attentional demands during a word recall and oculomotor dual task. *Front. Hum. Neurosci.* **9**, 381 (2015).
22. Maurer, U. *et al.* Frontal midline theta reflects individual task performance in a working memory task. *Brain Topogr.* **28**, 127–134 (2015).
23. Moran, R. J. *et al.* Peak frequency in the theta and alpha bands correlates with human working memory capacity. *Front. Hum. Neurosci.* **4**, (2010).
24. Roux, F., Wibral, M., Mohr, H. M., Singer, W. & Uhlhaas, P. J. Gamma-band activity in human prefrontal cortex codes for the number of relevant items maintained in working memory. *J. Neurosci.* **32**, 12411–12420 (2012).
25. Sghirripa, S. *et al.* Load-dependent modulation of alpha oscillations during working memory encoding and retention in young and older adults. *bioRxiv* 848127 (2019) https://doi.org/10.1101/848127.
26. Erickson, M. A., Smith, D., Albrecht, M. A. & Silverstein, S. Alpha-band desynchronization reflects memory-specific processes during visual change detection. *Psychophysiology* **56**, (2019).
27. Pahor, A. & Jausovec, N. Multifaceted pattern of neural efficiency in working memory capacity. *Intelligence* **65**, 23–34 (2017).
28. Zakrzewska, M. Z. & Brzezicka, A. Working memory capacity as a moderator of load-related frontal midline theta variability in Sternberg task. *Front. Hum. Neurosci.* **8**, 399 (2014).
29. Kofler, M. J., Rapport, M. D., Bolden, J., Sarver, D. E. & Raiker, J. S. ADHD and working memory: the impact of central executive deficits and exceeding storage/rehearsal capacity on observed inattentive behavior. *J. Abnorm. Child Psychol.* **38**, 149–161 (2010).
30. Unsworth, N. & Spillers, G. J. Working memory capacity: Attention control, secondary memory, or both? A direct test of the dual-component model. *J. Mem. Lang.* **62**, 392–406 (2010).
31. Wickham, H. *ggplot2: elegant graphics for data analysis.* (Springer, New York, 2016).
32. Engle, R. W. Working memory capacity as executive attention. *Curr. Dir. Psychol. Sci.* **11**, 19–23 (2002).
33. Shipstead, Z., Lindsey, D. R. B., Marshall, R. L. & Engle, R. W. The mechanisms of working memory capacity: primary memory, secondary memory, and attention control. *J. Mem. Lang.* **72**, 116–141 (2014).
34. Kotchoubey, B. Do event-related brain potentials reflect mental (cognitive) operations?. *J. Psychophysiol.* **16**, 129–149 (2002).
35. Luria, R., Balaban, H., Awh, E. & Vogel, E. K. The contralateral delay activity as a neural measure of visual working memory. *Neurosci. Biobehav. Rev.* **62**, 100–108 (2016).
36. Todd, J. J. & Marois, R. Capacity limit of visual short-term memory in human posterior parietal cortex. *Nature* **428**, 751–754 (2004).
37. Proskovec, A. L., Wiesman, A. I., Heinrichs-Graham, E. & Wilson, T. W. Beta oscillatory dynamics in the prefrontal and superior temporal cortices predict spatial working memory performance. *Sci. Rep.* **8**, 8488 (2018).
38. Proskovec, A. L., Wiesman, A. I., Heinrichs-Graham, E. & Wilson, T. W. Load effects on spatial working memory performance are linked to distributed alpha and beta oscillations. *Hum. Brain Mapp.* https://doi.org/10.1002/hbm.24625 (2019).
39. Grosbras, M.-H. & Paus, T. Transcranial magnetic stimulation of the human frontal eye field: effects on visual perception and attention. *J. Cogn. Neurosci.* **14**, 1109–1120 (2002).
40. Glahn, D. C. *et al.* Maintenance and manipulation in spatial working memory: dissociations in the prefrontal cortex. *NeuroImage* **17**, 201–213 (2002).
41. Christman, S. D., Garvey, K. J., Propper, R. E. & Phaneuf, K. A. Bilateral eye movements enhance the retrieval of episodic memories. *Neuropsychology* **17**, 221–229 (2003).
42. Lyle, K. B. & Edlin, J. M. Why does saccade execution increase episodic memory retrieval? A test of the top-down attentional control hypothesis. *Memory* **23**, 187–202 (2015).
43. Edlin, J. M. & Lyle, K. B. The effect of repetitive saccade execution on the attention network test: enhancing executive function with a flick of the eyes. *Brain Cogn.* **81**, 345–351 (2013).

44. Muggleton, N. G., Chen, C.-Y., Tzeng, O. J. L., Hung, D. L. & Juan, C.-H. Inhibitory control and the frontal eye fields. *J. Cogn. Neurosci.* **22**, 2804–2812 (2010).
45. Berman, M. G., Jonides, J. & Lewis, R. L. In search of decay in verbal short-term memory. *J. Exp. Psychol. Learn. Mem. Cogn.* **35**, 317–333 (2009).
46. Oberauer, K., Farrell, S., Jarrold, C. & Lewandowsky, S. What limits working memory capacity?. *Psychol. Bull.* **142**, 758 (2016).
47. Oberauer, K. *et al.* Benchmarks for models of short-term and working memory. *Psychol. Bull.* **144**, 885 (2018).
48. Camos, V. & Barrouillet, P. Attentional and non-attentional systems in the maintenance of verbal information in working memory: the executive and phonological loops. *Front. Hum. Neurosci.* **8**, (2014).
49. Bonnefond, M. & Jensen, O. Alpha oscillations serve to protect working memory maintenance against anticipated distracters. *Curr. Biol.* **22**, 1969–1974 (2012).
50. Sauseng, P. *et al.* Brain oscillatory substrates of visual short-term memory capacity. *Curr. Biol.* **19**, 1846–1852 (2009).
51. Palmer, J. A., Kreutz-Delgado, K. & Makeig, S. *AMICA: an adaptive mixture of independent component analyzers with shared components* (Swartz Cent. Comput. Neursoscience Univ. Calif, San Diego Tech Rep, 2012).
52. Delorme, A. & Makeig, S. EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *J. Neurosci. Methods* **134**, 9–21 (2004).
53. Oostenveld, R., Fries, P., Maris, E. & Schoffelen, J.-M. FieldTrip: open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Comput. Intell. Neurosci.* **2011**, 1 (2011).
54. Babu Henry Samuel, I., Wang, C., Hu, Z. & Ding, M. The frequency of alpha oscillations: Task-dependent modulation and its functional significance. *NeuroImage* **183**, 897–906 (2018).
55. Ikkai, A., Blacker, K. J., Lakshmanan, B. M., Ewen, J. B. & Courtney, S. M. Maintenance of relational information in working memory leads to suppression of the sensory cortex. *J. Neurophysiol.* **112**, 1903–1915 (2014).
56. van Gerven, M., Bahramisharif, A., Heskes, T. & Jensen, O. Selecting features for BCI control based on a covert spatial attention paradigm. *Neural Netw.* **22**, 1271–1277 (2009).
57. Barr, D. J., Levy, R., Scheepers, C. & Tily, H. J. Random effects structure for confirmatory hypothesis testing: Keep it maximal. *J. Mem. Lang.* **68**, 255–278 (2013).
58. Barr, D. J. Random effects structure for testing interactions in linear mixed-effects models. *Front. Psychol.* **4**, (2013).
59. Pavlov, Y. & Kochoubey, B. Oscillatory brain activity and maintenance of verbal working memory: a systematic review. PsyArXiv. https://doi.org/10.31234/osf.io/mn53j (2020).
60. Bates, D., Maechler, M., Bolker, B. & Walker, S. lme4: Linear mixed-effects models using Eigen and S4. *R Package Version* **1**, 1–23 (2014).
61. Kuznetsova, A., Brockhoff, P. B. & Christensen, R. H. B. lmerTest package: tests in linear mixed effects models. *J. Stat. Softw.* **82**, (2017).
62. Benjamin, D. J. *et al.* Redefine statistical significance. *Nat. Hum. Behav.* **2**, 6–10 (2018).
63. Miller, J. & Ulrich, R. The quest for an optimal alpha. *PLoS ONE* **14**, e0208631 (2019).
64. R Core Team. R: A language and environment for statistical computing. (2013).

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