

Report

Brain Oscillatory Substrates of Visual Short-Term Memory Capacity

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Summary

The amount of information that can be stored in visual short-term memory is strictly limited to about four items [1]. Therefore, memory capacity relies not only on the successful retention of relevant information but also on efficient suppression of distracting information, visual attention, and executive functions [2–5]. However, completely separable neural signatures for these memory capacity-limiting factors remain to be identified. Because of its functional diversity [6–9], oscillatory brain activity may offer a utile solution. In the present study, we show that capacity-determining mechanisms, namely retention of relevant information and suppression of distracting information, are based on neural substrates independent of each other: the successful maintenance of relevant material in short-term memory is associated with cross-frequency phase synchronization between theta (rhythmical neural activity around 5 Hz) and gamma (>50 Hz) oscillations at posterior parietal recording sites. On the other hand, electroencephalographic alpha activity (around 10 Hz) predicts memory capacity based on efficient suppression of irrelevant information in short-term memory. Moreover, repetitive transcranial magnetic stimulation at alpha frequency can modulate short-term memory capacity by influencing the ability to suppress distracting information. Taken together, the current study provides evidence for a double dissociation of brain oscillatory correlates of visual short-term memory capacity.

Results and Discussion

In two experiments, we recorded multichannel electroencephalograms (EEGs) from human volunteers while they performed visual working memory tasks (see [Supplemental Data](#)

available online) to determine electrophysiological correlates of short-term memory-limiting factors. Additionally, two repetitive transcranial magnetic stimulation (rTMS) experiments were conducted to further investigate the relevance of 10 Hz brain oscillations for short-term memory performance.

Experiment 1: Oscillatory Brain Activity Predicts Short-Term Memory Capacity

Bilateral arrays of colored squares (number of squares varied between two and six in each visual hemifield) were briefly presented. Subjects were asked to retain the color of squares of only one visual hemifield, which was previously signaled by a cue; the uncued items were to be ignored. The retained items had to be compared to a subsequent probe item. Within this experimental design, we analyzed oscillatory brain activity in the retention interval to identify and dissociate mechanisms that were responsible for retention of task-relevant stimuli and suppression of task-irrelevant visual stimuli.

Cross-Frequency Synchronization

Theta Phase-Locked Gamma Amplitude. In simulation studies as well as in electrophysiological experiments, interaction between theta (around 5 Hz) and gamma oscillations (>30 Hz) has been identified as a candidate for establishing memory functions in the brain [7, 10–13]. In particular, it has been shown that instantaneous theta phase has strong impact on instantaneous amplitude of high-frequency oscillations and multi- and single-unit activity [10, 14–16]. Based on this, high-frequency (20–70 Hz) EEG amplitude phase locked to theta (6 Hz) oscillations was investigated (see [15, 17, 18] and [Supplemental Data](#)) during the retention interval. If this estimate is high for a particular theta phase angle, there is a preference for increased gamma amplitude to occur always at this theta phase angle. As evidenced in [Figure 1A](#), a burst of high gamma activity (50–70 Hz) locked to the negative peak of theta was obtained for bilateral posterior parietal and occipital recording sites (this was revealed as a significant main effect for theta phase angle with high gamma amplitude as dependent variable by analysis of variance [ANOVA]; $F_{49/735} = 12.08$, $p = 0.000$). However, no effects of memory load (number of items to be retained), hemisphere, or visual hemifield (all main effects and interactions $p > 0.189$) were significant.

Neurocomputational models as well as electrophysiological data suggest multi-item memory results in gamma activity nested in theta cycles [6, 7, 10, 13, 15, 19–22]. Thus, gamma cycles represent single items that are bound together by a theta period. The question then arises as to why memory load did not affect theta phase-locked gamma amplitude. It is possible that when the number of retained items is increased, this is not necessarily reflected by increased amplitude of gamma frequency locked to theta. Instead, it might be indicated by more gamma cycles nested within one theta cycle [19, 20]. This should therefore be approached by a memory load-dependent modulation of either theta or gamma phase and should be visible in the exact phase locking between the two frequencies.

Phase Synchronization between Theta and Gamma. The strict synchronization between theta and gamma phase (not amplitude as above) might be more sensitive for highly

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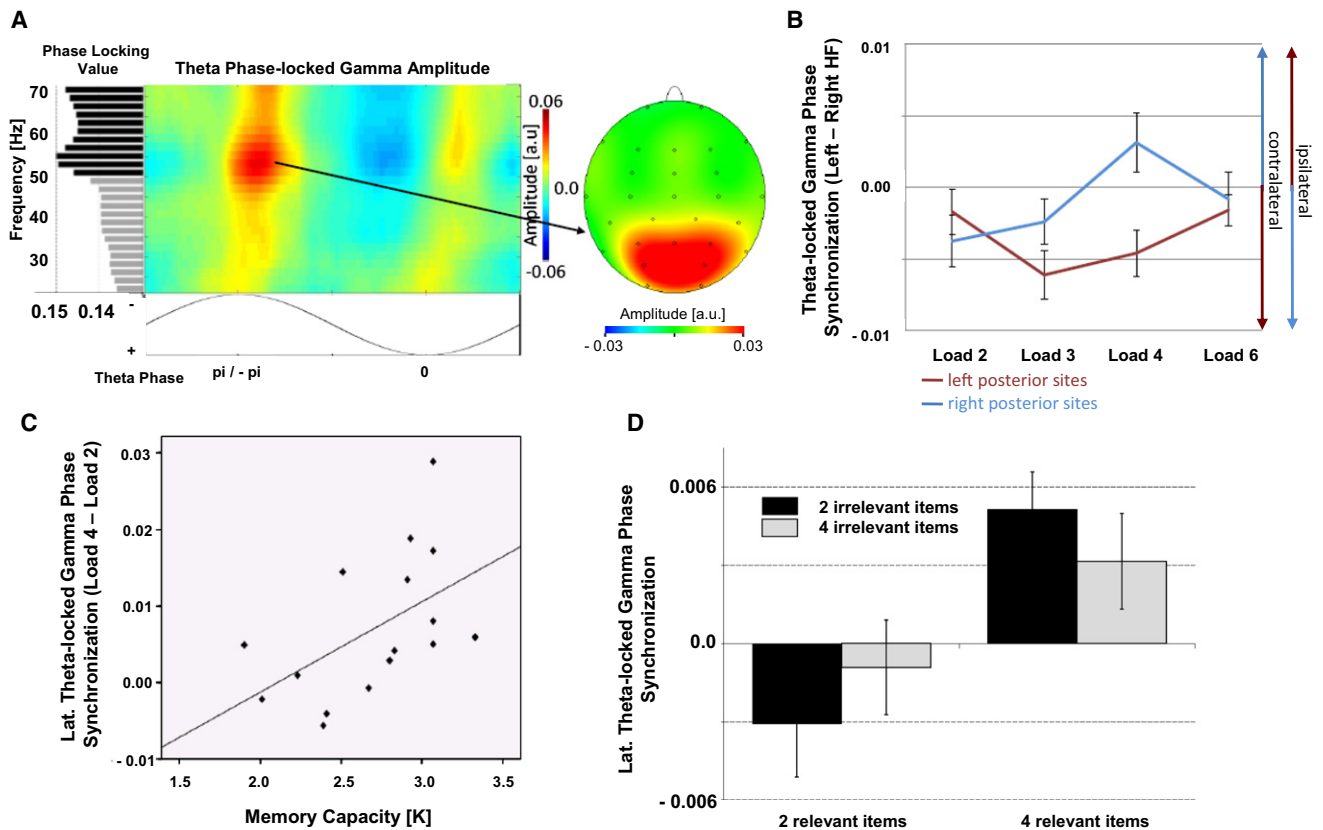


Figure 1. Theta-Locked Gamma Amplitude and Gamma Phase Synchronization

(A) Instantaneous amplitude values for frequencies >20 Hz were sorted according to instantaneous theta phase. Over bilateral posterior parietal and occipital recording sites, increased high gamma (50–70 Hz) amplitude is locked to the negative peak of a theta cycle. This is also indicated by significant phase-locking value [17]. Black bars at left indicate significantly higher coupling between theta phase and gamma amplitude for real than surrogate data.

(B) In contrast to theta-locked high gamma amplitude, theta-locked gamma phase synchronization dissociates memory loads and visual hemifields. Difference values between conditions with items from the left minus the right visual hemifield are depicted for memory loads 2, 3, 4, and 6. At left (red line) as well as right (blue line) posterior sites, there is a load-dependent increase of theta-locked gamma phase synchronization that occurs always contralateral to the retained information. The difference between contralateral and ipsilateral posterior sites is not significant for memory load 2, increases and becomes significant for loads 3 and 4 (with a maximum at load 4), and decreases again for load 6.

(C) The amount of this lateralized theta-locked gamma phase synchronization increase from memory load 2 to memory load 4 predicts individual short-term memory capacity, as indicated by a positive correlation.

(D) Results from experiment 2 indicate that lateralized theta-locked gamma phase synchronization is enhanced with increasing number of relevant items independent of the number of irrelevant items. Note that the difference between right and left posterior sites is depicted. Thus, positive values represent stronger contralateral theta-gamma phase synchronization. Errors bars in (B) and (D) represent standard errors of the mean.

specific cognitive processes [23–25]. Therefore, phase synchronization between theta and high gamma was calculated (for details, see Supplemental Data). This estimate describes the consistency of gamma phase in respect to instantaneous theta phase. Theta-gamma phase synchronization was only analyzed for the theta phase segment in which a significant phase-locked gamma burst (see Figure 1A) was revealed (one-sample t tests against 0: $t(15) > 4.07$, $p < 0.05$, corrected). The rationale for this was that instantaneous gamma phase is a reliable estimate if there is significant gamma activity present. Theta-gamma phase synchronization for intervals in which no gamma activity exists at all (i.e., gamma activity does not deviate from zero) would not be a meaningful measure. We expected theta-gamma phase synchronization to be increased at recording sites where relevant information was retained, thus, at contralateral posterior brain sites. Therefore, for each memory load, the difference of cross-frequency phase synchronization between contra- and ipsilateral was analyzed for left and right posterior recording

sites. Statistical analysis revealed a significant two-way interaction between memory load (2, 3, 4, or 6 items to retain) and hemisphere (left and right posterior recording sites) for theta-gamma phase synchronization ($F_{3/45} = 3.14$, $p = 0.034$). As indicated by post hoc Scheffé tests and depicted in Figure 1B, a significant ($p < 0.05$) increase of contralateral theta-locked gamma phase synchronization from memory load 2 to loads 4 and 6 was evidenced at right posterior sites. At left posterior sites, there was a significant contralateral theta-gamma phase synchronization increase (indicated by negative values) from memory load 2 to loads 3 and 4. A general lateralized increased theta-locked gamma phase synchronization can be estimated by the difference between left and right posterior recording sites. As shown in Figure 1B (and as underpinned by post hoc Scheffé tests), lateralized theta-locked gamma phase synchronization (i.e., the difference between left and right recording sites) was not significant for memory load 2 but increased significantly for load 3 and maximally for memory load 4. For memory load

6, left and right hemispheric recording sites no longer significantly differed.

With the exception of one subject, all participants in the experiment exhibited an estimated memory capacity between 2 and 4 (mean memory capacity = 2.70, standard error of the mean = 0.10). This suggests that contralateral theta-locked gamma phase synchronization increased in a load-dependent manner until memory capacity was approximately reached. When memory load exceeded memory capacity, gamma likely could not be nested into theta anymore, resulting in the drop back for memory load 6.

To investigate the relation between lateralized theta-locked gamma phase synchronization and memory capacity, we correlated the difference of lateralized cross-frequency phase synchronization between load 4 and load 2 with individual memory capacity. The rationale behind this was that a subject with a low memory capacity (e.g., 2) should not be able to increase lateralized theta-locked gamma phase synchronization beyond load 2, whereas a subject with (e.g.) memory capacity of 4 should be able to obtain an increase of lateralized theta-locked gamma phase synchronization up to load 4. As expected, a significant positive correlation between a lateralized load-dependent increase of theta-locked gamma phase synchronization and individual memory capacity was found ($r = 0.53$, $p = 0.036$; see [Figure 1C](#)).

Delta phase-locked and alpha phase-locked gamma amplitude or phase synchronization did not show any memory-related effects (see [Supplemental Data](#)).

EEG Alpha Amplitude

To perform well on a task like the one used in experiment 1, it is important not only to retain relevant information but also to efficiently suppress the retention of irrelevant items [3]. Deactivation or suppression of information processing is associated with oscillatory brain activity in the EEG alpha frequency range (around 10 Hz; see [26–32]). Thus, in the present experiment, it was expected that alpha power should be increased at posterior sites ipsilateral to relevant information as a correlate of irrelevant visual stimuli's suppression of processing. Taking into account that more irrelevant information had to be suppressed as memory load increased, we hypothesized that ipsilateral alpha power was enhanced with increasing memory load. [Figure 2A](#) depicts the topography of alpha amplitude for the difference between left and right visual hemifield in the four load conditions. It is evident that only left and right posterior recording sites exhibited hemifield-specific differences of alpha amplitude. Two-way ANOVA revealed a significant interaction ($F_{3/45} = 5.60$, $p = 0.002$) between memory load (2, 3, 4, or 6 items to retain) and hemisphere (left and right posterior recording sites). Post hoc Scheffé tests yielded significant increase of ipsilateral alpha amplitude from memory load 2 to loads 3, 4, and 6 at left posterior recording sites (indicated by positive values), and a significant ipsilateral increase was evident for right posterior sites from memory load 2 to loads 3 and 4 (indicated by negative values; see [Figure 2B](#)). This suggests that in contrast to theta-gamma phase synchronization, alpha band amplitude was always higher ipsilateral to the retained memory items than contralateral, and this difference increased from memory load 2 to loads 3, 4, and 6. If the suppression of distractor item retention could increase efficiency of short-term memory processes and was reflected by alpha amplitude, lateralized alpha activity should also predict individual memory capacity. Based on this assumption, the difference of lateralized alpha amplitude (but now ipsilateral minus contralateral) between memory

load 4 and memory load 2 was correlated with individual memory capacity. A significant positive correlation was obtained ($r = 0.68$, $p = 0.004$; see [Figure 3C](#)). Thus, alpha band amplitude appears to correlate with individual capacity based on suppression of irrelevant information.

Experiment 2: Separate Neural Correlates for Distinct Capacity-Limiting Mechanisms

Experiment 1 suggested that theta-gamma phase synchronization and alpha amplitude are neural correlates of short-term memory capacity, the former based on retention of relevant information and the latter based on suppression of irrelevant information. However, in experiment 1, the number of relevant and irrelevant items in each visual hemifield was always the same, making this dissociation difficult. Therefore, a second EEG experiment was run in which the amount of relevant and irrelevant information was varied. Four conditions were used: (1) two items in the attended hemifield and two in the unattended hemifield (two relevant, two irrelevant), (2) two items in the attended visual field and four in the unattended visual field (two relevant, four irrelevant), (3) four relevant items and two irrelevant items, or (4) four relevant and four irrelevant items (see [Supplemental Data](#) for details). The same EEG analyses as implemented for experiment 1 were run for experiment 2.

Theta-Gamma Phase Synchronization and Retention of Relevant Information

As can be seen in [Figure 1D](#), lateralized posterior theta-locked gamma phase synchronization was higher in conditions with four relevant items compared to only two. A significant interaction, relevant information \times hemisphere, was obtained ($F_{1/13} = 5.438$, $p = 0.036$; note that in [Figure 1D](#), the difference between right and left posterior sites is depicted; thus, positive values represent stronger contralateral theta-gamma phase synchronization). No main effect or interaction involving the factor irrelevant information was found to be significant (all $p > 0.134$). This shows that, as suggested by experiment 1, phase synchronization between theta and high gamma oscillations responds to retention of relevant information exclusively, independent of the amount of irrelevant information.

Alpha Amplitudes and Suppression of Irrelevant Information

Ipsilateral alpha amplitudes during the retention interval were mainly influenced by the amount of irrelevant information that had to be suppressed. As indicated by a significant interaction between the factors irrelevant information and hemisphere ($F_{1/13} = 7.295$, $p = 0.018$) and as shown in [Figure 2D](#), there was higher ipsilateral alpha activity in conditions with four irrelevant items compared to only two (note that in [Figure 2D](#), the graphs represent hemispheric differences in lateralized alpha power; higher positive values reflect stronger ipsilateral alpha activity). This result was statistically independent of the amount of relevant information. No main effect or interaction involving the factor relevant information was significant. The interaction between relevant information and hemisphere, however, showed a tendency toward significance ($p = 0.078$). One can therefore argue that alpha amplitude also seems to be at least minimally involved in the processing of relevant information. There are three explanations for this effect. First, it might be possible that increased alpha activity also plays a role in specific mnemonic processes [9, 33]. This should in particular account for evoked alpha activity [34, 35]. However, in the current analysis, only induced alpha activity was investigated, leaving this interpretation rather

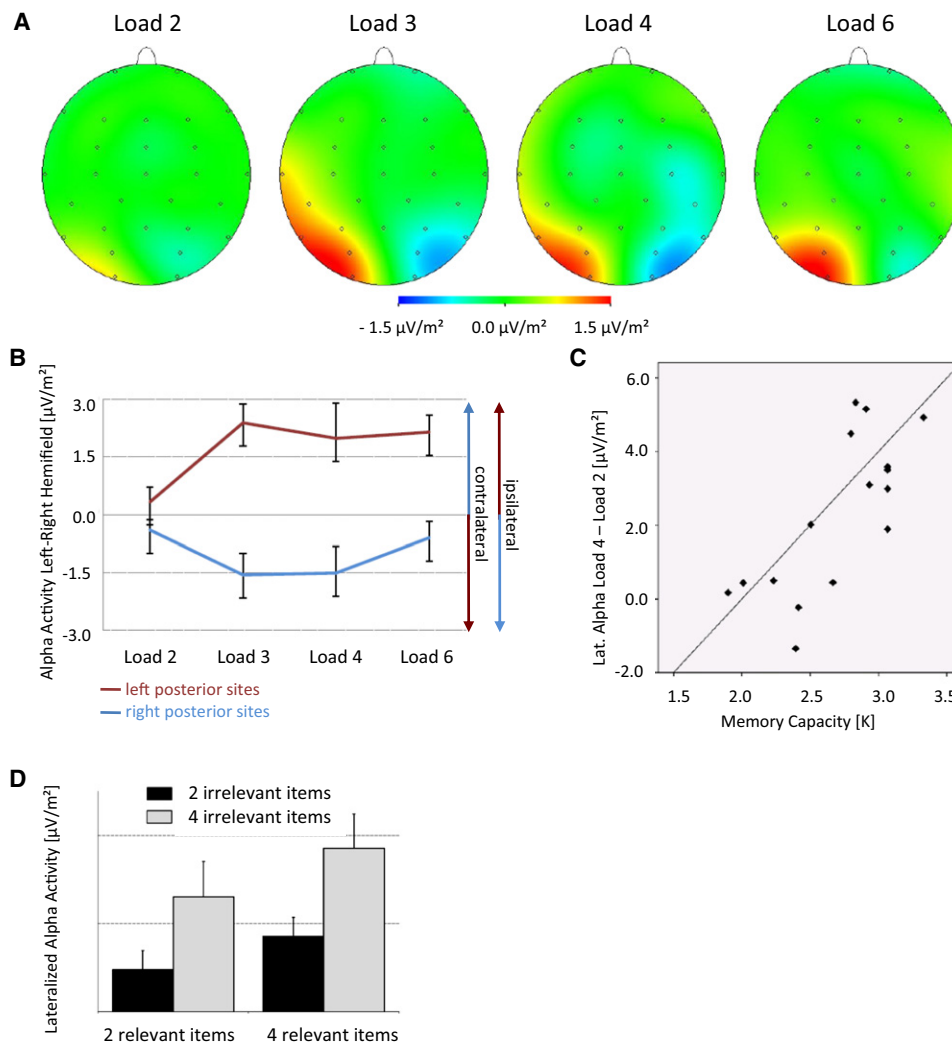


Figure 2. EEG Alpha Activity in the Retention Interval Predicts Memory Capacity

(A) Topographic maps of alpha amplitude differences between “left items retained” and “right items retained” show clear lateralization at posterior recording sites, with stronger alpha amplitudes ipsilateral to retained items.

(B) This lateralized alpha activity increases from memory load 2 to loads 3, 4, and 6.

(C) Lateralized alpha amplitude increase from memory load 2 to load 4 predicts individual short-term memory capacity. But note that, in contrast to theta-locked gamma phase synchronization, alpha amplitude is increased at ipsilateral recording sites and thus rather reflects processing of irrelevant items.

(D) Ipsilateral alpha activity is associated with the amount of irrelevant information that has to be suppressed. As indicated by experiment 2, this effect is largely independent of the amount of relevant information held in memory. Note that the bars represent hemispheric differences in lateralized alpha power; higher positive values reflect stronger ipsilateral alpha activity. Errors bars in (B) and (D) represent standard errors of the mean.

unlikely. A more plausible explanation is that there was more visuospatial attention directed to a hemifield where more targets were presented, leading to stronger contralateral alpha amplitude reduction [29, 30] and therefore to increased lateralized alpha activity for conditions with a high amount of relevant information. A third explanation is simply that attention to four items led to stronger contralateral alpha power reduction than only two items solely as a result of increased visual input independent of any attentional processes. However, note that none of these assumptions can explain the much stronger (inhibitory) alpha response to irrelevant information. Thus, results from experiment 2 definitely appear to underpin the double dissociation already suggested by experiment 1, with theta-locked gamma phase synchronization and alpha amplitude being two independent neural correlates of short-term memory capacity.

Experiment 3: Modulation of Short-Term Memory Capacity via rTMS

In experiment 3, we used rTMS to test whether the relation between the lateralized increase in parietal alpha power and memory capacity was beyond a simple correlative association. A similar type of task was used as in experiment 1. During the retention interval, rTMS was delivered with 10 Hz to parietal sites either contralateral or ipsilateral to the items that had to be retained. There is evidence that rTMS can entrain alpha amplitude at the stimulated cortical region [36, 37]. Therefore, 10 Hz rTMS ipsilateral to retained items should support effective suppression of irrelevant items by mimicking increased ipsilateral alpha amplitude as seen in the EEG study. As a consequence, it should increase memory capacity. Contralateral rTMS, on the other hand, should prevent successful maintenance of relevant information and thus decrease

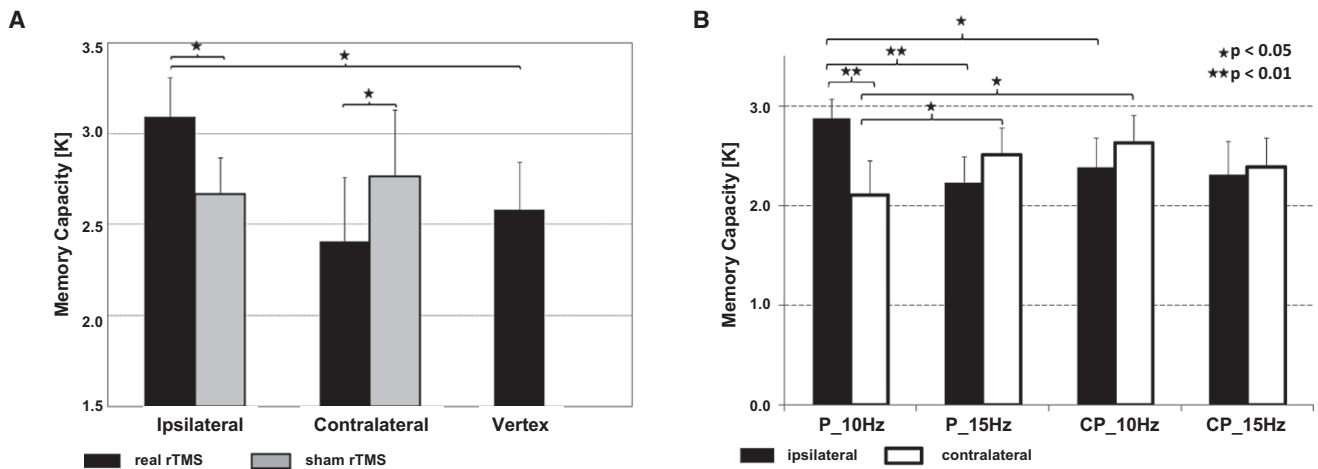


Figure 3. rTMS at 10 Hz over Ipsilateral Posterior Parietal Cortex Increases Memory Capacity

(A) Results from experiment 3. When real repetitive transcranial magnetic stimulation (rTMS) (black bars) at 10 Hz is delivered during the retention interval at posterior parietal sites ipsilateral to the retained items, memory capacity is increased compared to control stimulation (gray bars) and compared to verum rTMS at the vertex. rTMS applied at contralateral sites leads to decreased memory capacity compared to control stimulation.

(B) Results from experiment 4. Only rTMS at 10 Hz over parietal sites (P_10Hz) leads to increased memory capacity when applied ipsilaterally and to decreased capacity when applied contralaterally. For parietal and centroparietal stimulation at 15 Hz (P_15Hz and CP_15Hz) or rTMS at 10 Hz over centroparietal sites (CP_10Hz), no such effect is found. Errors bars represent standard errors of the mean.

memory capacity. As a control condition, stimulation with a tilted coil was applied at posterior parietal sites [38, 39]. Furthermore, to control for discomfort and rTMS-induced sensations, real rTMS was delivered to the vertex. This stimulation condition should be similar in discomfort compared with parietal rTMS without having an impact on task performance.

One-way ANOVA comparing all conditions revealed a significant main effect ($F_{4/24} = 4.418$, $p = 0.008$; Figure 3A) for stimulation on memory capacity. Post hoc Scheffé tests suggested that, compared to the control conditions, memory capacity was significantly increased when real rTMS was delivered over ipsilateral (to memory-relevant items) posterior parietal cortex. On the other hand, contralateral posterior parietal rTMS led to a decrease in memory capacity. The control conditions did not differ significantly from each other.

Thus, when memory-related EEG alpha activity patterns are used as the basis for rTMS stimulation parameters, short-term memory capacity can be altered. However, it was not completely clear from this experiment which mechanism was responsible for the alternation of memory capacity: it could be entrainment of alpha activity by 10 Hz rTMS (as shown in a recent study [40]), or alternatively, it could be competitive interaction between hemispheres [41] with disinhibition of one hemisphere in response to rTMS of the other one. To further investigate this, we conducted experiment 4.

Experiment 4: Frequency-Specific Effect of rTMS

Similar to experiment 3, 10 Hz rTMS was applied to ipsilateral or contralateral posterior parietal sites. However, to investigate frequency specificity of the effect, 15 Hz rTMS was also delivered. As control conditions, the same kind of stimulation was applied to centroparietal sites. As shown in Figure 3B, only 10 Hz rTMS at posterior parietal sites increased memory capacity when applied ipsilateral to relevant items, whereas it had a detrimental effect on memory capacity when delivered contralaterally. This effect was absent with rTMS at 15 Hz or

with centroparietal 10 Hz rTMS (significant interaction site \times frequency \times hemifield: $F_{1/12} = 23.331$, $p = 0.000$).

These results suggest that entrainment of alpha activity by 10 Hz rTMS might be the physiological basis of the observed behavioral effects. Competitive hemispheric biasing as the underlying mechanism responsible for altered memory capacity seems to be less likely. Otherwise, similar results should have been obtained with 15 Hz stimulation. However, the present study can only provide indirect evidence for these conclusions, and we can only speculate about the exact underlying mechanisms. It will be necessary to investigate the direct impact of 10 Hz rTMS on EEG activity in the alpha frequency band in further research (similar to the approach described by Hamidi and colleagues [40]).

Conclusions

Vogel and coworkers [2, 3] elegantly demonstrated that lateralized slow cortical negativity at posterior brain regions predicts memory capacity. However, these studies did not enable the dissociation of mechanisms related to information selection and the neural principles of memory storage per se that are necessary for a better understanding of the limitations of memory capacity. In contrast to this, we propose based on the present results that the retention of visual information is reflected by gamma-theta interaction at posterior parietal sites. Synchronization of gamma phase to the negative peak of theta oscillations (1) was increased contralaterally to the visual hemifield containing relevant items to be retained, (2) showed a load-dependent enhancement up to where average memory capacity was reached, and (3) predicted individual short-term memory capacity. A similar pattern was also found for alpha amplitude, with the difference that these results (1) were found ipsilateral to relevant items and (2) reflected suppression of irrelevant information. Experiment 2 showed that these two neural mechanisms for retention of relevant information and suppression of irrelevant information are largely independent of each other.

The two rTMS experiments demonstrated that short-term memory capacity is modulated by rTMS at the posterior parietal cortex. When rhythmic magnetic stimulation at 10 Hz was applied to sites where irrelevant information has been processed, memory capacity was increased. Experiment 4 provided indirect evidence that the basic mechanism might be entrainment of alpha amplitudes at the stimulation site, because there was a frequency-specific effect for 10 Hz rTMS. However, because no direct influence of rTMS on alpha activity was investigated, this interpretation remains speculative.

In the present study, similar to research by Vogel and coworkers [2, 3], effects were found only for posterior recording sites. However, this does not necessarily indicate that the frontal cortex is not involved in visual short-term memory. The strong perceptual component of the task probably highlights effects in visual cortex. The prefrontal cortex, on the other hand, might be important for monitoring and initiation of the described local posterior neural correlates of short-term memory processes [42–45]. Therefore, although we found two different neural correlates for short-term memory retention of relevant information and suppression of irrelevant information, there are still a large number of cognitive functions that may also limit information processing capacity [4]. Similar to the approach used in the present study, it will be important for future research to separate the neural correlates of these memory-relevant processes, which might, in a further step, be modulated externally. This could be beneficial for applied and clinical neurosciences in patients with selective cognitive dysfunctions that attenuate short-term memory capacity and during normal aging.

Supplemental Data

Supplemental Data include Supplemental Experimental Procedures, Supplemental Results, and seven figures and can be found with this article online at [http://www.cell.com/current-biology/supplemental/S0960-9822\(09\)01859-4](http://www.cell.com/current-biology/supplemental/S0960-9822(09)01859-4).

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