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Separate oscillatory mechanisms support fragile visual short-term memory and visual working memory

CHAPTER 3

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Abstract

Evidence is accumulating that the classic two-stage model of Visual Short-Term Memory (VSTM), comprising Iconic Memory (IM) and Visual Working Memory (WM), is incomplete (Sligte et al., 2008; Vandenbroucke et al., 2011). A third memory stage, termed Fragile Visual Short-Term Memory (FM) seems to lie in between IM and WM. Although FM can be distinguished from IM using behavioral and fMRI methods, the question remains whether FM is a weak expression of WM or a separate form of memory with its own neural signature. Here, we tested whether FM and WM in humans are supported by dissociable time-frequency features of electroencephalography (EEG) recordings. Subjects performed a partial-report change detection task, from which individual differences in FM and WM capacity were estimated. These individual FM and WM capacities were correlated with the time-frequency characteristics of the EEG signal before and during encoding of the memory display. FM capacity correlated with an increase in theta power in central-parietal electrodes during encoding. FM was also related to an increase in frontal gamma that occurred simultaneously with a decrease in peri-occipital alpha before onset of the memory display, suggesting that an increase in visual excitability is more important for FM than for WM. Together, these data show that FM depends more on visual processing mechanisms than does WM, thus providing novel evidence for a dissociation between these VSTM stages.

Introduction

Traditionally, Visual Short-Term Memory (VSTM) has been divided into two subsystems: a short-lasting, but large capacity storage termed Iconic Memory (IM; Sperling, 1960; Neisser, 1967) and a long-lasting, but small capacity storage termed Visual Working Memory (WM; Luck et al., 1996). In the last decade, evidence for a third memory stage that operates in between IM and WM, termed Fragile Visual Short-Term Memory (FM; Griffin & Nobre, 2003; Landman et al., 2003; Makovski et al., 2008; Sligte et al., 2008). However, while FM can be clearly dissociated from IM (Sligte et al., 2008), it remains a topic of debate whether FM is really different from WM (Makovski, 2012; Matsukura & Hollingworth, 2011).

FM is distinct from IM, as it has a smaller capacity and lasts for several seconds (Lewis-Peacock, Drysdale, Oberauer, & Postle, 2012; Sligte et al., 2008). Moreover, in contrast to IM, FM is not erased by a light mask (Sligte et al., 2008), and neural traces associated with FM have been found in V4, showing that these representations are based on cortical processing and not on retinal afterimages (Sligte et al., 2009). At the same time, FM seems to differ from WM, since the presentation of a display containing similar stimuli overwrites FM representations, while it does not overwrite WM (Pinto et al., 2013; Sligte et al., 2008). Second, when attention is diverted during memory encoding, FM capacity reduces only slightly, while WM capacity suffers considerably (Vandenbroucke et al., 2011). Also, when TMS is applied over the Dorsolateral Prefrontal Cortex during maintenance, WM capacity decreases, while FM capacity remains intact (Sligte et al., 2010). Therefore, we suggest that FM reflects a stage in VSTM in which visual cortical icons are maintained independent of focused attention, whereas information in WM has received selective attention, thereby making the information more robust and available for further manipulation and report (Sligte et al., 2010).

Although behavioral evidence is accumulating that FM and WM reflect different stages in VSTM, it could be that FM is merely a weak form of WM and depends on the same neural substrates. Here, we recorded EEG while subjects performed a partial-report change detection task that measures FM and WM capacity (Fig. 3.1). To measure FM capacity, a spatial cue is presented after offset of the memory display, but before onset of the test display (Fig. 3.1A). This way, all items that are processed up to a visual cortical level and are not yet overwritten by new stimulation can be retrieved. To measure WM, the spatial cue is only presented after onset of the test display. Hereby, all FM representations are overwritten and only items that are made robust against interference are available for report (Fig. 3.1B). Crucially, to investigate the difference between FM and WM mechanisms, we correlated individual FM and WM capacity with oscillatory activity *before* onset of the cue. If FM representations are indeed formed

separately from WM representations, a difference in the underlying oscillatory mechanisms should already be evident before the spatial cue is used to access FM.

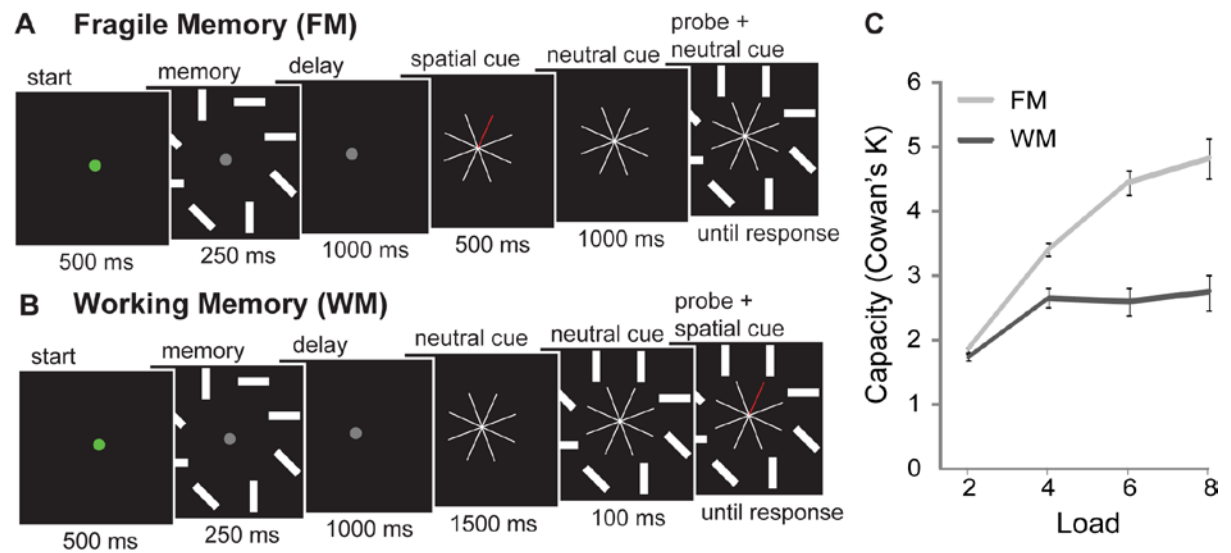


Figure 3.1. Task design and behavioral results. Subjects were instructed to remember all rectangles in the display. On FM trials (A), a spatial retro-cue was presented that indicated which item might change orientation at test (50% change). On WM trials (B), instead of a spatial cue, a neutral cue was presented. The spatial cue was presented after appearance of the test display. The presentation of the test display will erase FM memory traces and leave only WM representations intact. C) Capacity for FM (light grey) and WM (dark grey) on the 4 different loads. Capacity differs between FM and WM trials. Also, FM capacity increases with memory load, while for WM it reaches plateau at a load of 4.

Methods

Subjects

Twenty-five students (Mean age = 23, SD = 2, 11 male) from the University of Amsterdam participated in this experiment for course credit or monetary reward. All subjects had normal or corrected-to-normal vision and signed an informed consent form before participation. The study was approved by the local Ethics Committee.

Stimuli

Memory and test displays consisted of white rectangles ($1.4^\circ \times 0.4^\circ$ in visual degrees) presented on a black background, placed radially (2.6°) in eight invisible placeholders. The rectangles had four possible orientations: horizontal, vertical, 45° rotated to the horizontal or 135° to the horizontal. The neutral cue consisted of a white star (total span 2.4°) containing eight arms

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pointing towards the 8 possible item locations. To create the spatial cue, one of the eight white arms was replaced by a red arm (Fig. 3.1A and B).

Task & Procedure

To indicate the start of a trial, the grey fixation dot turned green for 500 ms. Then, the memory display appeared for 250 ms containing 2, 4, 6 or 8 oriented rectangles placed randomly in the eight placeholders (Fig. 3.1A and B). Subjects were instructed to remember the orientation of all rectangles. On FM trials (Fig. 3.1A), a spatial retro-cue was presented 1000 ms after offset of the memory array, indicating which item could change in the test display (50% change, 90° rotation, all other items remained unchanged). After 500 ms, the retro-cue was replaced by a neutral cue. The test display was presented 1000 ms after offset of the retro-cue and subjects indicated whether they perceived an orientation change in the cued memory item. WM trials started the same as FM trials (Fig. 3.1B), but instead of presenting a spatial cue 1000 ms after offset of the memory array, a neutral cue was presented for 1500 ms. The spatial cue was then presented 100 ms after onset of the test display. All trials were separated by a 1000 ms inter-trial interval.

Before the start of the EEG recordings, subjects received two training blocks of 64 trials (FM: 32, WM: 32, randomly intermixed). Importantly, subjects were not prompted to which trial type they would receive. The probability of a trial containing 2, 4, 6 or 8 rectangles was equal, but randomly distributed within blocks (8 trials for each load in FM and WM). After the training trials, subjects performed 384 trials for each condition (96 trials per load; total of 768 trials), separated in blocks of 64 trials.

Behavioral analyses

To determine FM and WM capacity Cowan's K was calculated ($(\text{hit rate} - 0.5 + \text{correct rejection} - 0.5) * N$), which corrects for guessing (Cowan, 2001). To investigate the correlation between behavior and time-frequency characteristics, maximum FM and WM capacity for each subject were taken as the maximum score on any of the 4 loads (P. Sauseng et al., 2009). This reflects individual FM and WM capacity most reliably, because when load heavily exceeds memory capacity (for example in the load 8 WM condition), subjects might underperform compared to their true capacity.

EEG recordings & preprocessing

EEG was recorded at 1024 Hz using a 64-channel Biosemi ActiveTwo system (BioSemi, Amsterdam, the Netherlands) placed according to the 10-20 system. Offline, data were down-

sampled to 512 Hz, high-pass filtered at 0.5 Hz, and re-referenced to the average of two earlobes electrodes. Trials were epoched from -1.5 to 4 seconds (relative to the onset of the memory array). Due to a recording error, for two subjects only 512 trials were recorded. All trials were visually inspected, and trials containing artifacts not related to eyeblinks were removed. One subject was removed because of an excessive number of artifacts, leaving too little trials to analyze. For the remaining 24 subjects, an average of 7.8 % of the trials was removed (ranging from 1.6 % to 22.6 %, SD = 5.5 %), leaving a minimum of 59 trials per load per memory condition, and a minimum of 244 trials per overall memory condition. To remove eyeblink artifacts, an Independent Component Analysis was performed for each subject and components that were clearly related to eyeblinks were removed using EEGLab (Delorme & Makeig, 2004). After component removal, we applied a spatial filter (current-source-density) that increases topographical selectivity by filtering out spatially broad and therefore likely volume-conducted effects (Srinivasan, Winter, Ding, & Nunez, 2007). The units of data after this transformation are mV/cm².

EEG Time-Frequency Decomposition

All data were analyzed using Matlab 2010 (MathWorks Inc.) in combination with EEGLab (Delorme & Makeig, 2004). We convolved the time domain signal with a complex Morlet wavelet with increasing cycles as frequency increased (Cohen, Elger, & Ranganath, 2007; Cohen, van Gaal, & Lamme, 2009). The resulting complex signal provided an estimate of power for each time point at 30 frequencies between 2 and 70 Hz (logarithmically spaced). Epochs were centered at the onset of the memory array and relatively large windows were taken (-1.5 to 4 seconds) to prevent edge artifacts from contaminating the estimates of power. Power was normalized using a decibel (dB) transform, for which the baseline was taken as the average power over each frequency band at -1000 to -600 ms (grey fixation) for each condition. This way, data from each subject and each condition are in the same scale and thus comparable.

Electrode selection

Because we did not have any a priori hypotheses regarding the electrodes at which we would find correlates between brain and FM/WM, we selected electrodes by visually inspecting power data after onset of the memory array (Fig. 3.2). To prevent a bias towards choosing electrodes that showed a difference in FM and WM, thereby increasing the chances to find a significant difference between conditions (Kriegeskorte, Simmons, Bellgowan, & Baker, 2009), we inspected power averaged over all subjects and conditions. We selected four sites (electrode sets) that

showed the most pronounced changes in power after onset of the memory display (Fig. 3.2A). As we did not expect any lateralization effects, because memory items were presented on both sides of the fixation cross, we pooled together the two visual sites, creating 3 electrode sites (peri-occipital: PO3/4, PO7/8, P5/6, P7/8; central-parietal: Pz, CPz; midfrontal: FCz, FC1/2) on which to base further analyses.

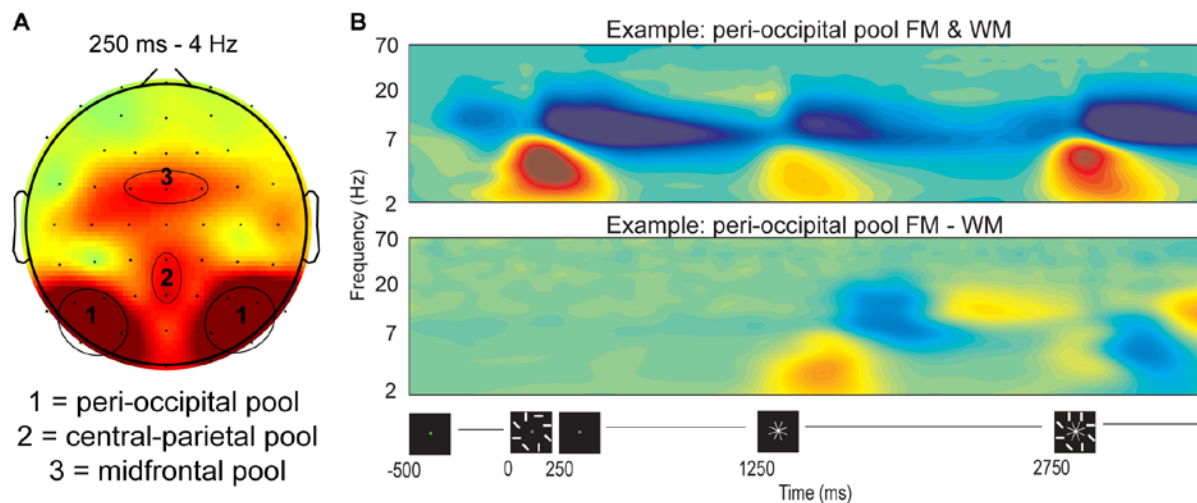


Figure 3.2. Electrode selection. A) Based on the response associated with the memory array at 250 ms (4 Hz), three electrode poolings were made to investigate correlations between power and FM/WM capacity. B). Example of average power (upper) and power difference (lower) for the peri-occipital pool. For illustrative purposes, the whole trial is depicted here, but only data between the indication of the start of a trial (-500 ms) and the cue (1250, neutral or spatial) were used for the correlational analyses.

Correlation analyses

To investigate the oscillatory mechanisms underlying FM and WM capacity, we correlated the maximum FM/WM capacity per subject with the average power on FM/WM trials at each frequency band and at each time point before onset of the retro-cue, creating a correlational time-frequency plot for each electrode pooling (using Spearman's Rho, R). To compare the difference between FM and WM, we transformed the correlations using Fisher's Z, which allows the comparison of non-normally distributed data (Fisher et al., 1970). To determine time-frequency windows of interest, we split the data in half, using the odd trials as a selection set. Because we were specifically interested in the difference between FM and WM, we selected time-frequency points from the selection set that had a Fisher's Z difference between FM and WM of at least 1.96 (corresponding to a two-sided p-value of .05). We drew windows around

these time-frequency points (see Fig. 3.4A) and used the even trials (test set) to statistically evaluate the difference between FM and WM correlations. We tested this difference using a permutation test, shuffling the mapping between subjects' capacities and their EEG data 10,000 times, and calculated how many times the new correlation difference exceeded the original correlation difference (corresponding to a p-value).

The above procedure allowed for a rigorous statistical test of differences between FM and WM correlations with EEG power (Nieuwenhuis, Forstmann, & Wagenmakers, 2011). However, we were primarily interested in how FM and WM capacity correlate individually with EEG. Therefore, when the original correlation difference was significant ($p < .05$), we evaluated whether there was a clear relation between either FM or WM capacity with power in the significant time windows. Because FM and WM capacity were correlated ($R = .44$, $p = .03$), we also computed partial correlations (that is, correlating WM capacity while partialling out FM capacity, and vice versa). We then permuted single FM and WM correlations, thus calculating a p-value for both memory types separately.

To investigate whether between-subject differences in FM and WM correlations were due to inter-individual trait differences or to intra-individual state differences, we conducted a second analysis on the significant time-frequency windows. Within each subject, we ranked all FM and WM trials according to power (not baseline corrected), divided the data into one low- and one high-power trial set, and calculated capacity over these two sets. If the between-subject correlations between FM and WM capacity and power were state-dependent, one would expect to find a capacity difference between low- and high-power trials. If, however, the difference in neural mechanisms underlying FM and WM capacity reflects trait differences, there should be no difference in capacity between low- and high-power trials.

Results

Behavioral results

Using a 2 (Memory: FM, WM) x 4 (Load: 2, 4, 6, 8) Repeated Measures ANOVA, we found a main effect of Memory, showing that FM capacity was larger than WM capacity (Fig. 3.1C; $F(1,3) = 98.8$, $p < .001$). Also, there was an interaction effect between Memory and Load ($F(1.8, 41.2) = 27.5$, $p < .001$), showing that WM capacity increased between load 2 and 4 ($t(23) = 7.8$, $p < .001$), but not between load 4 and 6 or between load 6 and 8 ($t(23) = -.3$, $p = .736$; $t(23) = .7$, $p = .473$), while FM capacity increased until load 6 (difference between load 4 and 6: $t(23) = 7.7$, $p < .001$), and then leveled off between load 6 and 8 ($t(23) = 1.8$, $p = .093$). This confirms previous work showing that FM has a larger capacity than WM, and that FM performance can increase with

larger memory load, while WM capacity stays fixed even when increasing the number of items to remember (Sligte et al., 2008).

Correlation between capacity and power

To investigate whether FM and WM depend on different underlying oscillatory mechanisms, we correlated individual FM and WM capacity with time-frequency power *before* onset of the cue. Importantly, subjects were not aware of the trial type they would receive before onset of the cue, and thus could not prepare for the two conditions differently. We confirmed that indeed no significant differences were found in power before onset of the retro-cue between FM and WM trials when averaged over subjects (Fig. 3.2B). However, if different mechanisms support the formation of representations in FM and WM, a divergence should be seen before onset of the retro-cue when we correlate individual differences in time-frequency power with individual FM and WM capacity.

We first calculated the correlation between FM capacity and average power on all odd FM trials, and between WM capacity and average power on all odd WM trials (selection set, see Methods). As we wanted to specifically test the difference between FM and WM, we selected time-frequency windows that showed a significant difference between FM and WM in the selection set. We then tested whether there was a significant difference between FM and WM for these time-frequency windows in the even trials.

There were four time-frequency windows that showed a significant difference in correlation between FM and WM (Fig. 3.4A). We therefore explored the correlations for these 4 windows for FM and WM separately by calculating their partial correlation values, which reflect the correlation between FM capacity and power when WM capacity is taken into account and vice versa (see Methods). For the peri-occipital pool, there was a negative correlation with FM capacity for 6-18 Hz (alpha) power before onset of the test display (-500 to 0 ms, window 1), whereas there was no correlation with WM capacity (FM: $R = -.49$, WM: $R = .08$; FM – WM difference: $p = .02$). Also in peri-occipital channels, the 2-3 Hz (delta) power just before and during presentation of the test display (-100 to 100 ms, window 2) correlated more positively with FM than with WM (FM: $R = .62$, WM: $R = .30$; FM – WM difference: $p = .04$). For the central-parietal pool, there was a significant difference for 3-7 Hz (theta) after onset of the memory display (0 to 400 ms, window 3) that showed a positive correlation with FM and a slightly negative correlation with WM (FM: $R = .59$, WM: $R = -.09$; FM – WM difference: $p = .002$). Last, in the midfrontal pool, a window of 37-70 Hz (gamma) power before onset of the memory display (-500 to 0, window 4) correlated positively with FM and negatively with WM (FM: $R = .32$, WM: R

= -.29; FM – WM difference: $p = .01$). Together, these data show that FM capacity is at least partially related to different oscillatory mechanisms than WM capacity. Crucially, these differences arise even before onset of the retro-cue, which suggests that the build-up of FM and WM representations is supported by divergent mechanisms.

Interestingly, both the peri-occipital and midfrontal pool showed a strong correlation with FM before onset of the memory display (Fig. 3.4, window 1 and 4). To investigate whether there was a relation between individual midfrontal gamma power and peri-occipital alpha power, we correlated the average power for FM trials in these two time-frequency windows and tested significance using a permutation test in which individual power for the peri-occipital pool was shuffled 10,000 times. Because this was a post-hoc test, we employed an α of .001. The correlation between midfrontal gamma and peri-occipital alpha was significant ($R = -.65$, $p = .0006$), showing that when midfrontal gamma was higher, peri-occipital alpha was lower. This suggests that a top-down mechanism operating between midfrontal and peri-occipital channels regulates the expectancy of the memory display, thereby increasing FM capacity, but not WM capacity. Both time-frequency windows did not correlate with any of the other time-frequency windows (all $p > .09$).

Although we found 3 positive correlations for FM, we did not find any positive correlations for WM. We therefore tested the variance of FM and WM capacity to see whether a larger variance in FM could explain this difference. Variance of FM (1.5) and WM (1.1) were significantly equal, however (Levene's statistic = .7, $p = .41$), and therefore cannot fully explain this finding.

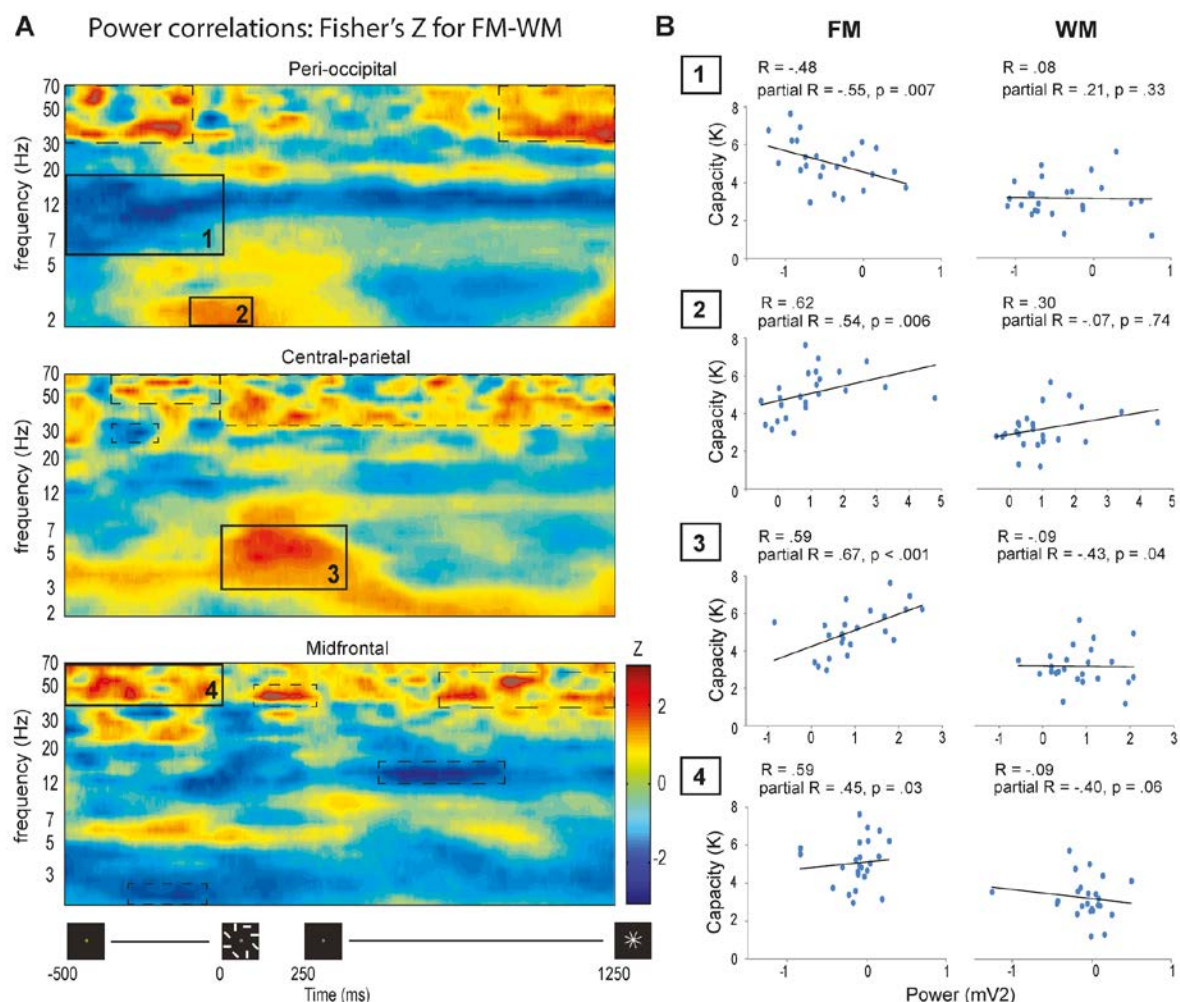


Figure 3.4. Correlation between power and capacity. A) Time-frequency plots showing the difference between FM and WM correlations with power on the odd trials. Plots depict the time from the indication of the start of a trial (green fixation dot, -500 ms) to the onset of the cue (1250 ms). Based on the Fisher's Z values for the odd trials, thirteen windows were selected to test for significance in the even trials. Dotted squares indicate 9 windows that were selected and tested, but were not significant in the even trials. In four windows (solid squares, numbered), a significant difference between Fragile Memory (FM) and Working Memory (WM) correlations was found. B) The relation between power on the even trials and FM and WM capacity for the four significant time windows. Plots depict the full correlations (R), but partial correlations (partial R , displayed above the plots) were calculated from the residuals when regressing out WM capacity for the FM correlation and vice versa. The numbers correspond to the time windows in A.

The current correlational differences between FM and WM were based on between-subject analyses. The question remains whether these differences reflect inter-individual trait

differences or intra-individual state differences. We therefore divided the data of the 4 time-frequency windows into low- and high-power trial sets, and calculated capacity over the low and high-power sets separately. We conducted four 2 (Memory: FM, WM) x 2 (Power: Low, High) ANOVAs, and found that only in time-frequency window 1 (peri-occipital alpha, -500 to 0 ms), there was a main effect of Power ($F(1,23) = 11.3$, $p = .003$, 3 other time-frequency windows, all $F(1,23) < .4$, all $p > .58$). This indicates that when subjects had lower alpha during the indication of the start of the trial, they performed the memory task better on both FM and WM trials. However, we found no significant interactions between Memory and Power (all $F(1,23) < 3.8$, all $p > .06$), suggesting that the correlational differences between FM and WM capacity and power were due to subjects' general trait characteristics.

Discussion

Over the last years, several studies have shown that the traditional two-stage system of Visual Short-Term Memory (VSTM), comprising Iconic Memory (IM) and Working Memory (WM), might be insufficient (Pinto et al., 2013; Sligte et al., 2008; Vandembroucke et al., 2011). A third stage of VSTM, termed Fragile Memory (FM), has been proposed to lie in between IM and WM. FM can be clearly dissociated from classical IM, since it has a smaller capacity, does not rely on retinal afterimages (Sligte et al., 2008) and has a cortical basis (Sligte et al., 2009). In the present study, we showed that FM and WM can be dissociated on the basis of their electrophysiological correlates. We found several time-frequency windows before onset of the retro-cue for which power correlated differently with FM and WM capacity. This shows that the mechanisms at play during encoding of the memory array differently determined the formation of FM and WM representations.

The first difference between FM and WM was evident before onset of the memory display. When the fixation dot turned green to alert subjects to the start of a trial, FM capacity correlated negatively with peri-occipital alpha power (6-18 Hz). A pre-stimulus decrease in occipital alpha has been related to visual discriminability (van Dijk et al., 2008), visual attention (Klimesch, 1999; Sauseng et al., 2005), and visual excitability (Lange, Oostenveld, & Fries, 2013). In the same time window, FM correlated positively with frontal gamma (37-70 Hz) power. An increase in frontal gamma before stimulus onset - also in combination with a decrease in posterior alpha - has been shown to modulate reaction time to visual stimuli (Gonzalez Andino, Michel, Thut, Landis, & Grave de Peralta, 2005). In the current study, the increase in frontal gamma power correlated with the decrease in peri-occipital alpha power. This indicates that a top-down mechanism might have controlled the state of visual readiness to encode information,

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and this state of readiness facilitated FM representations to be formed, but did not relate to the formation of WM representations.

After stimulus onset a positive correlation between FM and theta power (3-7 Hz) and a negative correlation between WM and theta power were found for the central-parietal electrode pool. At the same time, an increase in delta power (2-3 Hz) correlated more positively with FM for the peri-occipital pool. An increase in power after stimulus presentation at these electrode sites is related to visual processing of the memory display (Klimesch, 1999). Thus, subjects with enhanced visual processing of the memory items had a larger FM capacity, but not a larger WM capacity. This indicates that forming FM representations is more dependent on visual processing of a scene than the forming of WM representations is.

The variance between subjects in the power spectra which resulted in a difference in FM and WM capacity is suggested to reflect a general trait difference between subjects rather than the state a subject is in during a particular trial. Multiple studies have shown that differences in time-frequency spectra can be related to differences in white matter density (Cohen, 2011a; Cohen, 2011b; Valdés-Hernández et al., 2010; Zaehle & Herrmann, 2011). It could thus be that in the current study, a difference in structural connectivity between areas involved in this task was the underlying source of the correlation between power and capacity.

The current study shows that the formation of FM and WM at least partly rely on different mechanisms. FM has a clear visual basis, while for WM, visual processing of the memory display is less important. In the model we propose (Sligte et al., 2010), FM represents the maintenance of items at a visual level, while WM reflects maintenance of items on a cognitive, perhaps more abstract level. The capacity to maintain items at a visual level is much larger than the capacity to maintain items at a cognitive level, depending on the complexity of the items that are used (Sligte et al., 2010; Vandenbroucke, Sligte, Fahrenfort, Ambroziak, & Lamme, 2012). In conclusion, these results show that a distinction between Fragile Visual Memory and Visual Working Memory, and thus a distinction between three different stages (Iconic, Fragile, and Working Memory) in VSTM, is warranted.

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