The quality of perception without attention

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Manipulations of attention dissociate fragile visual short-term memory from visual working memory

CHAPTER 2

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Abstract

People often rely on information that is no longer in view, but maintained in visual short-term memory (VSTM). Traditionally, VSTM is thought to operate on either a short time-scale with high capacity – iconic memory - or a long time scale with small capacity – visual working memory. Recent research suggests that in addition, an intermediate stage of memory in between iconic memory and visual working memory exists. This intermediate stage has a large capacity and a lifetime of several seconds, but is easily overwritten by new stimulation. We therefore termed it fragile VSTM. In previous studies, fragile VSTM has been dissociated from iconic memory by the characteristics of the memory trace. In the present study, we dissociated fragile VSTM from visual working memory by showing a differentiation in their dependency on attention. A decrease in attention during presentation of the stimulus array greatly reduced the capacity of visual working memory, while this had only a small effect on the capacity of fragile VSTM. We conclude that fragile VSTM is a separate memory store from visual working memory. Thus, a tripartite division of VSTM appears to be in place, comprising iconic memory, fragile VSTM and visual working memory.

Introduction

Classical theories on visual short-term memory (VSTM) generally make a distinction between iconic memory and working memory. Iconic memory is a high-capacity store that lasts for about half a second and is easily overwritten (Averbach & Coriell, 1961; Sperling, 1960), while visual working memory is low in capacity, lasts seconds to minutes and is resistant against visual interference (Luck & Vogel, 1997; Phillips, 1974). Recent research, however, suggests that there might be an additional short-term memory stage in between iconic memory and visual working memory (Becker et al., 2000; Griffin & Nobre, 2003; Landman et al., 2003, 2004; Makovski & Jiang, 2007; Sligte et al., 2008, 2009; 2010). This stage has been shown to have a large capacity and a lifetime of up to four seconds (Lepsien, Griffin, Devlin, & Nobre, 2005; Sligte et al., 2008, 2009). At the same time, it is easily overwritten by similar visual stimulation. We believe this stage reflects storage of information in a fragile format and propose to term it fragile VSTM.

Previous studies have already shown that fragile VSTM can be dissociated from the classical notion of iconic memory. The lifetime of fragile VSTM by far outlasts the lifetime of iconic memory (Lepsien et al., 2005; Sligte et al., 2008, 2009) . When a cue is shown after stimulus presentation, items can be retrieved from fragile VSTM for up to 4 seconds, which is much longer than the 500 ms decay time for iconic memory (Averbach & Coriell, 1961; Sperling, 1960). The two memory stores also seem to rely on different characteristics. When objects are presented in an isoluminant colour compared to their background, the capacity of iconic memory decreases, while that of fragile VSTM remains the same. Moreover, a flash of light presented directly after stimulus presentation has a decreasing effect on iconic memory, but not on fragile VSTM. This suggests that iconic memory relies on contrast differences, while fragile VSTM does not (Sligte et al., 2008). Finally, it has been shown that perceptual grouping and segregation occurs in fragile VSTM (Landman et al., 2003, 2004).

Whether fragile VSTM can be dissociated from visual working memory, however, remains an open question. At first sight, it seems the two have different behavioral and psychophysical characteristics. The capacity of fragile VSTM can be up to four times as high as the capacity of visual working memory and fragile VSTM is completely overwritten by objects that are similar to those presented in the memory display, whereas visual working memory is resistant to overwriting (Sligte et al., 2008). In neural terms, however, the distinction is not so clear. A recent fMRI study showed that V4 activity was related to storage in both fragile VSTM and visual working memory, but when an item was represented in visual working memory, activity was higher in a retinotopically specific way (Sligte et al., 2009). This might suggest that fragile VSTM is just a weakly represented form of visual working memory.

If this is the case, it could be that fragile VSTM is supported by the same neural substrate as visual working memory, but that activity related to fragile VSTM is just below threshold for report. Another possibility is that fragile VSTM represents the underlying storage capacity of VSTM, while visual working memory corresponds to a robust store that relies on attention to boost sensory information and make it available for cognitive manipulations and report. If that is the case, fragile VSTM could be formed without the need for attentional selection, while visual working memory actually depends on attentional selection to be formed. Neurally, this distinction can be sustained; fragile VSTM might be supported by higher visual and inferotemporal areas that are often linked to memory encoding or maintenance (Todd & Marois, 2004; Tseng et al., 2010; Xu & Chun, 2005), while visual working memory might be supported by extended brain regions involved in attention, selection and control, seated mainly in the parietal and prefrontal cortex (Curtis & D'Esposito, 2003; Lepsien et al., 2005; Pessoa, Gutierrez, Bandettini, & Ungerleider, 2002; Ranganath & D’Esposito, 2005). Recent research from our lab suggests that at least the dorsolateral prefrontal cortex (DLPFC) is not involved in the storage of fragile VSTM; when TMS is applied over the right DLPFC, visual working memory suffers, but fragile VSTM remains unaffected (Sligte et al., 2011). Preliminary evidence thus implies that the two memory stores can be separated. If visual working memory indeed heavily depends on attention and control processes while fragile VSTM does not, then disrupting these processes behaviorally would yield the same results: visual working memory capacity decreases, while fragile VSTM should stay relatively intact.

To test this hypothesis, we diverted attention during presentation of a memory array, while subjects performed a change detection task that measures both the capacity of fragile VSTM and the capacity of visual working memory (Fig. 2.1). All our attention manipulations were aimed at disrupting attention during encoding, although the early stages of maintenance might also have been affected, especially in the second experiment. Previous studies have shown a tight relationship between top-down attention and visual working memory maintenance (Awh et al., 2006; Fougnie, 2008). Nevertheless, it has not been explicitly investigated whether attention during encoding and/or maintenance is necessary for the build-up and maintenance of fragile VSTM representations. Only one study provides preliminary evidence that attention is not necessary for maintenance of fragile VSTM (Landman et al., 2003). This study suggests that these representations do not depend on attention by showing that even after attentionally selecting a specific item from VSTM, non-selected items could still be retrieved. This implies that items remain available in fragile VSTM, even when attention is diverted. In the current study, we used three different attention manipulations to examine whether decreased attention during presentation of the memory display has a dissociating effect on fragile VSTM and visual working memory.

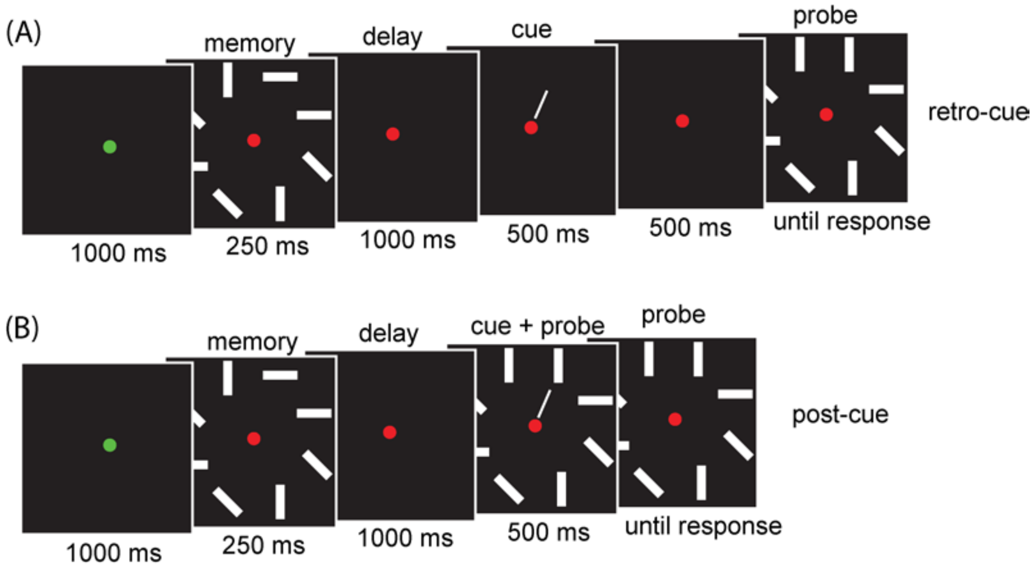

Figure 2.1. General trial design. *On each trial, subjects had to retain the orientation of eight rectangles across a retention interval. After the retention interval, one of the rectangles changed orientation on 50 percent of the trials and subjects had to detect this change. On each trial, a cue singled out the item to change, either A) during the retention interval (retro-cue) to measure fragile VSTM or B) during the probe array (post-cue) to measure visual working memory.*

In the first experiment, temporal uncertainty for presentation of the memory array was created. It has been shown that when attention is not properly oriented in time, performance suffers (Coull, Frith, Buchel, & Nobre, 2000; Small et al., 2003). We used this temporal aspect of attention by presenting subjects multiple memory arrays of which only one had to be compared to the test array. Subjects did not know which memory array would be the last one and thus the one to maintain in memory, and therefore were not able to fully orient their attention. We observed that visual working memory capacity decreased, while fragile VSTM remained intact. In a second experiment, subjects performed an n-back task prior to and during the delivery of the display to remember. In this dual-task setting, visual working memory capacity also suffered more than fragile VSTM. In a third experiment the change detection task was combined with an Attentional Blink (AB) paradigm (Olivers, van der Stigchel, & Hulleman, 2007; Raymond et al., 1992; Shapiro, 2009). In an AB paradigm, subjects have to detect two targets in a stream of distracter items. When the second target is presented in proximity of the first target, detection of the second target suffers. This decrease in detection is attributed to a lapse in attention due to processing of the first target. We used the AB to reduce attention on the memory array. Again, the decline in performance was larger for visual working memory than for fragile VSTM. Together, these results indicate that when attention is occupied, visual working memory suffers, but fragile VSTM stays relatively intact. This study thus supports the notion of two separate processes in memory: one that is engaged in the storage of information and one that is responsible for the selection of information through attention.

General Methods

The general set-up of all experiments described in this paper is identical; in each experiment, we presented human volunteers with a cued change detection task (Becker et al., 2000; Griffin & Nobre, 2003; Landman et al., 2003; Makovski & Jiang, 2007; Sligte et al., 2008, 2009; Sligte, Vandenbroucke, et al., 2010) that is able to measure the capacity of fragile VSTM and the capacity of visual working memory in a single experiment. Differences between experiments are how we manipulated attention during presentation of the stimuli to remember, namely by (1) creating uncertainty, by (2) having a dual-task set-up, and by (3) creating an Attentional Blink.

Participants

In total, 30 students of the University of Amsterdam participated in two training sessions that preceded the main experiments (see *Training* of General Methods). All participants had normal or corrected-to-normal vision. For their participation, subjects received course credits or a monetary reward. The local ethics committee of the University of Amsterdam had approved the study and participants gave their written informed consent before the start of the experiment.

Stimuli and apparatus

Stimuli were presented on a 19-in. Ilyama monitor at a refresh rate of 60 Hz. Participants were seated 100 cm away from the screen, resulting in a total display size of 20.4 by 15.4 degrees in visual angle. Objects in each visual array were white rectangles (1.56 by 0.39 degrees of visual angle) placed on a black background, radially at four degrees of visual angle from a fixation point. The memory and probe arrays contained eight of these rectangles that each had one of four possible orientations; horizontal, vertical, 45˚ to the horizontal or 135˚ to the horizontal. Cues consisted of white lines (2.55 by 0.06 degrees of visual angle) that pointed from the fixation point to one of the eight possible locations.

Design and procedure

Participants were instructed to maintain fixation at a red dot in the middle of the screen throughout each trial. At the start of each trial, the red fixation dot turned green for 1000 ms. After this, the memory array containing eight oriented rectangles appeared for 250 ms. Participants were instructed to remember the orientations of the rectangles in this memory array to their best ability. There were two types of trials (see Fig. 2.1). On retro-cue trials, a 500-ms cue was presented 1000 ms after offset of the memory array and this cue indicated which of the eight rectangles might change orientation between memory and probe array. Another 1000 ms later, the probe array would appear and participants had to indicate by button press whether the cued rectangle had changed orientation compared to the memory array or not (Fig. 2.1a). These trials measured fragile VSTM. On post-change cue trials, the 500-ms cue was not delivered during the retention interval, but simultaneously with the probe array, 1000 ms after offset of the memory array (Fig. 2.1b). These trials measured visual working memory. The post-change cue was presented to keep this condition comparable to the retro-cue condition. Thus, on both trials, the 500-ms cue was presented 1000 ms after offset of the memory array.

The probe array remained on screen until participants gave a response by pressing one of two buttons positioned on the right armrest of the chair. The left button was always associated with no-change responses and the right button with change response. Participants were instructed to always press the no-change button, unless they were absolutely sure they had seen a change. After each response, participants received auditory feedback indicating whether they had performed correctly. In addition, participants were informed that the cue was always valid and none of the other rectangles could change orientation. The change always consisted of a 90˚ rotation and occurred on 50 % of both types of trials. All trials were randomly mixed within blocks.

Training

Prior to participation on all of the three experiments, participants received training on the cued change detection task. Participants received two sessions of training and only those participants with a mean percentage correct of at least 80% were allowed to participate in the experiments reported in the rest of the paper. This decreased the probability of floor effects (50 %; chance performance) that might occur in the dual-task setting.

In the two training sessions, the difficulty of the task was gradually increased until it reached its final form as described in the previous section. In the first 64 trials, the memory array remained on screen for 500 ms instead of 250 ms and the cue was presented at an interval of

100 ms after offset of the memory array. For the next 64 trials, the memory array was presented for 250 ms and the cue was given 500 ms after memory array offset. Participants then practiced 184 trials of the task with its final settings on the first session and another 480 trials during the second session. Each 60 trials, subjects were allowed to pause and they received feedback on their total performance level. Participants that did not reach a mean score of 80% after the second session received course credits or a monetary reward for their participation, but were not allowed to participate in the final experiments. Out of 30 participants, 7 subjects did not reach this 80% criterion.

Experiment 1

Previous research has shown that attention can be manipulated temporally (Coull et al., 2000; Nobre, 2001; Small et al., 2003). When a target stimulus is presented at an unexpected point in time, detection performance suffers. In the current task, we used this temporal aspect of attention to decrease attention for the memory array. Subjects were presented with a random number of different rectangle arrays (1-7) and only the last array served as the memory array (Fig. 2.2). Therefore, subjects never knew before the start of a trial how many arrays would appear. We expected that because subjects could not properly prepare themselves for the memory array, attention for this array would be diminished (however, see Discussion for more considerations). If attention is only necessary for visual working memory, but not for fragile VSTM, performance should only decrease in the post-change cue condition.

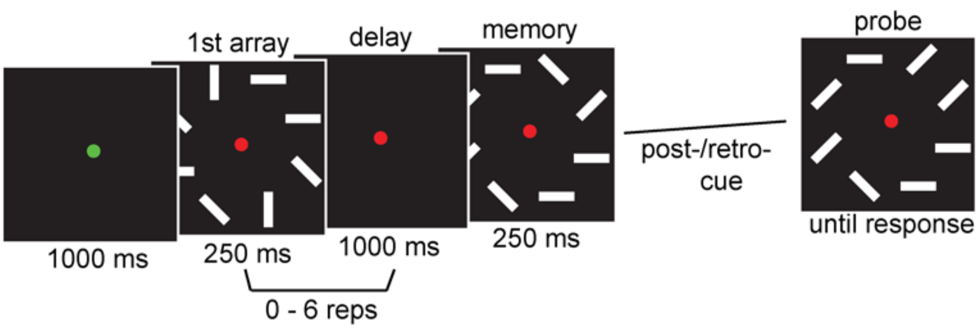

Figure 2.2. Experiment 1: Trial design. *At the start of a trial, 1 - 7 arrays containing different rectangle configurations were presented. Only the last array served as the memory array. Participants never knew how many arrays would appear and thus never knew whether the presented array would be the memory array. After presentation of the memory array, the trial proceeded as a post- or a retro-cue trial.*

Methods

Subjects

Out of the 23 participants that passed the training, 12 took part in Experiment 1 (age 17 – 27).

Stimuli and apparatus

Stimuli and apparatus are described in *Stimuli and apparatus* of the General Methods.

Design and procedure

Every trial started with the red fixation dot turning green for 1000 ms after which the first rectangle array was presented for 250 ms. After offset of this first array, there was a 1000 ms black screen. After this delay, either the cue was presented (retro or post-change) or another rectangle array was presented for 250 ms (Fig. 2.2). If the cue was presented, the participant had to indicate whether in the probe array, the rectangle in this location had changed orientation compared to the memory array. If another rectangle array was presented, the participant was instructed to remember the orientations of this new array. So, the probe array always had to be compared to the last rectangle array shown. On every trial, 1 – 7 arrays could be presented.

At the start of the experiment, participants received 96 trials of the basic cued change detection task (48 retro-cue and 48 post-cue, mixed) as described in *Design and Procedure* of the General Methods. This served as a pre-test for the participants' basic memory capacity. After this, they received 14 practice trials and 336 experimental trials of the Multiple Array (MA) change detection task. For each number of arrays (1-7), there were 48 trials (24 retro-cue, 24 post-cue). On 50% of the trials, the cued rectangle changed orientation. All trials were randomly mixed. At the end of the experiment, participants again received 96 trials (48 retro-cue and 48 post-cue) of the basic cued change detection task. This served as a post-test for their memory capacity.

Analysis

We calculated memory capacity by computing Cowan's K (Cowan, 2001). The formula is K = ((percentage hits – 0.5) + (percentage correct rejections – 0.5)) * N items, and accounts for guessing by subtracting 50 % change performance. To determine the effect of the MA manipulation, we performed a repeated measures ANOVA on Cowan's K for memory type (fragile VSTM, visual working memory) X task (pre-test, MA, post-test) .

Results

The results replicated previous findings that fragile VSTM has a larger capacity than visual working memory (Fig. 2.3, $F(1,11)=64.0$, $p<.001$) (Landman et al., 2003; Sligte et al., 2008, 2009; 2010). The MA task had a decreasing effect on capacity for both types of memory ($F(1,11)=62.2$, $p<.001$, all paired t-test $p<.05$). However, the MA task had a much larger effect on visual working memory than on fragile VSTM ($F(2,22)=10.1$, $p=.001$). The reduction was on average (pre-test and post-test) 0.67 items for fragile VSTM and 1.82 items for visual working memory, which corresponds to a reduction of 9.7 % for fragile VSTM and 33.7 % for visual working memory. This effect was driven by a difference in both pre-test compared to MA task ($F(1,17)=13.2$, $p=.004$) and MA task compared to post-test ($F(1,11)=14.3$, $p=.003$).

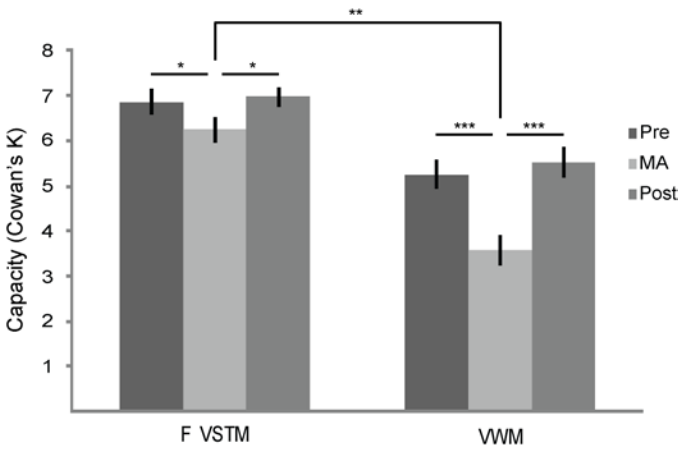

Figure 2.3. Experiment 1: Results. *Performance on fragile VSTM (F VSTM) and visual working memory (VWM) trials (expressed as capacity, Cowan's K) for the pre-test, Multiple Array (MA) task and post-test. Performance on the MA task was worse for both types of memory, but VWM suffered more than F VSTM. * p < .05, ** p < .01, *** p < .001*

Average performance on the fragile VSTM trials was rather high (Cowan's K pre-test = 6.86, post-test = 6.97). It could be that the interaction effect was driven by ceiling performance on the fragile VSTM trials of the pre- and post-test. To investigate this, we correlated fragile VSTM capacity of the pre-test and post-test with the decline in capacity of fragile VSTM during the MA-task (Fig. S2.1). If the effect would be driven by ceiling performance, this would result in a negative correlation; decline in performance would be smallest for the high-performers and largest for the low-performers. This was not the case. Even with a considerable spread in performance for the fragile VSTM trials, correlations between pre-test capacity and MA capacity decrease or post-test capacity and MA capacity decrease were not significant (Pearson's R=.326, p=.301; Pearson's R=.245, p=.442).

Discussion

In Experiment 1, attention for the memory array in a cued change detection task was decreased by creating uncertainty for when the task relevant memory array would be presented. This manipulation had a larger effect on visual working memory than on fragile VSTM. Research has shown that just as with spatial attention, the prefrontal cortex modulates temporal attention (Coull et al., 2000; Nobre, 2001; Small et al., 2003). We therefore infer that when attentional resources are not optimally directed, visual working memory suffers because the frontal brain areas can exert less control over the lower visual areas that modulate the storage of information. Fragile VSTM capacity, however, possibly depends on lower level areas and might therefore be less affected by this manipulation.

Although we hypothesized that the attention manipulation would not affect fragile VSTM capacity at all, there was a small and significant reduction in performance (K = .67). It can be debated whether the manipulation effectively influenced temporal attention. Other factors, such as proactive interference - the negative influence of similar arrays preceding the memory array -, might also have played a role. For instance, if visual working memory for the previous arrays was not properly cleared, the lingering effect of wrongly remembered items would affect both fragile VSTM and visual working memory. However, this effect would be much stronger for visual working memory, as this is a low-capacity store, while the effect on fragile VSTM would be less pronounced. A suggestion for future research might be to exploit the temporal allocation of attention by varying the temporal certainty of the memory array.

Experiment 2

In Experiment 1, the temporal aspect of attention was manipulated. Here, we manipulated central attention by having subjects perform a Rapid Serial Visual Presentation (RSVP) task. Subjects had to respond when in a letter stream an identical letter was presented 1 or 2 positions back, also known as an n-back task (Fig. 2.4). The memory array was presented while participants performed the n-back task, so they could not fully attend to the memory array. We expected, again, that this attention manipulation would have a larger effect on visual working memory than on fragile VSTM. Moreover, we expected that the 2-back task would be more attention demanding than the 1-back task. We therefore predicted that performance on the change detection task would suffer more from the 2-back task and that this decrement would be larger for visual working memory than for fragile VSTM.

Methods

Subjects

Out of the 23 participants that passed the training, 18 took part in experiment 2 (age 17 – 27). Of these 18 participants, 9 took part in experiment 1 as well.

Stimuli and apparatus

Stimuli and apparatus are described in *Stimuli and apparatus* of the General Methods.

Design

A green fixation dot indicated the start of a trial. A sequence of letters was then presented at the position of the fixation point (Fig. 2.4). Each letter was presented for 300 ms with an ISI of 300 ms. After 7, 11 or 13 letters (distributed evenly over all trials), the memory array was presented together with a letter for 300 ms. After another 300 ms ISI, the last letter appeared. The cue (retro or post-change) was presented 1000 ms after the last letter, so the interval between cue and memory array was now 1600 ms.

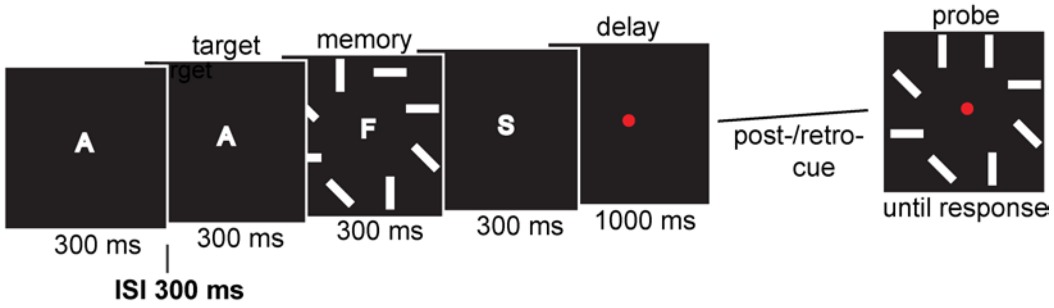

Figure 2.4. Experiment 2: Trial Design. Change detection combined with an n-back task. *A trial started with a stream of 9, 13 or 15 letters. During the one to last letter, the memory array was presented. Subjects had to detect an immediate letter repetition (1-back, depicted) or a letter repetition with one different letter in between (2-back). After the last letter, the trial proceeded as a post- or a retro-cue trial.*

Experiment 2 consisted of two different testing sessions. In the first session, the letter sequences were set up so that it was a 1-back task: participants had to press the button positioned on the left armrest when they saw the same letter presented in the sequence as one position before. In the second session, the letter sequence was set up so that it was a 2-back task: now participants had to detect a repetition of a letter that was shown two positions back. Per trial, there were 1 to 3 letter targets and on 33.3% of the trials, a target was presented one position before, during, or one position after the memory array. There were no 1-back repetitions during the 2-back task. In both sessions, the secondary task was to answer whether one of the rectangles had changed orientation in the probe array. As a repetition of a letter could also occur during or after presentation of the memory array, participants were forced to keep paying attention to the letter sequence, even when the memory array was shown. They were told that the letter task was the most important task and that they should try to score 100 % on this task.

Each of the two sessions started with a practice block on the basic change detection (96 trials: 48 retro cue, 48 post cue) and a basic n-back task. In the basic n-back task, a letter stream was presented for 30 seconds and 90 seconds without the memory array surrounding it. Then, subjects performed the dual task three times. Once, subjects only had to respond to the n-back task and ignore the memory and probe arrays (24 trials). This served as the basic n-back score. Once, subjects only had to respond to the change detection task and ignore the letters (12 practice trials, 144 experimental trials: 72 retro-cue, 72 post-cue). This will be referred to as the single task, and served as the basic memory capacity score. To measure the effect of the n-back task on memory capacity, subjects had to respond to the two tasks at the same time (dual task), treating the n-back task as the main task (12 practice trials, 144 experimental trials: 72 retro-cue, 72 post-cue). The three experimental tasks were counterbalanced between subjects to prevent any sequence effects.

Analyses

As in Experiment 1, Cowan's K for memory capacity was calculated (see *Analyses* for Experiment 1). In the dual task, the trials in which a letter target was presented one position before, during, or one position after the memory array (33.33%) were taken out of the analyses because pressing a button during presentation of the memory or probe array might interfere with the perceptual processing itself. The corresponding trials in the single task were left out as well. A repeated measures ANOVA analysis using Cowan's K was done for the variables of memory type (fragile VSTM , visual working memory) X task demand (single, dual) X n-back (1,2). To examine the performance on the n-back task, a repeated measure ANOVA on percentage correct for n-back (1,2) X task demand (single, dual) X memory type (visual working memory, fragile VSTM) was performed.

Results

In Experiment 2, subjects performed a dual-task with an n-back task as primary task. Performance on the n-back task did not differ between the single- and dual-task setting ($F(1,17)=0.033$, $p=.857$), suggesting that subjects followed the instructions and treated the n-back task as their primary task. Percentage correct on the 1-back was higher than on the 2-back task ($F(1,17)=24.6$, $p=.001$), which indicates that as intended, the 2-back task was more difficult. Importantly, performance on the n-back did not differ between the two types of memory trials ($F(1,17)=0.002$, $p=.964$).

As in Experiment 1, fragile VSTM capacity was larger than visual working memory capacity ($F(1,17)=361.8$, $p<.001$). There was a general decrease in capacity for both types of memory when a secondary task was performed (Fig. 2.5, $F(1,17)=58.6$, $p<.001$). Again, this effect was larger for visual working memory than for fragile VSTM ($F(1,17)=28.6$, $p<.001$). The reduction averaged over both n-back conditions was 0.51 (reduction of 6.9 %) items for fragile VSTM and 1.89 (reduction of 36.3 %) for visual working memory. Performing a secondary task thus had a larger effect on visual working memory than on fragile VSTM.

The three-way interaction between n-back, task demand and memory type did not reveal a statistically significant effect ($F(1,17)=1.9$, $p=.181$), suggesting that performing a 2-back task did not have a larger effect on visual working memory than on fragile VSTM compared to performing a 1-back task. Looking at Figure 2.5 however, performing a 2-back task seems to produce a statistically larger effect for fragile VSTM, but a numerically larger effect on visual working memory. As the three-way interaction might not have enough power to detect these differences, we chose to perform a repeated measure ANOVA on n-back (1,2) X demand (single, dual) for fragile VSTM and visual working memory separately. Both types of memory suffered from performing a dual task (fragile VSTM, $F(1,17)=7.6$, $p=.013$; visual working memory, $F(1,17)=73.9$, $p<.001$). However, fragile VSTM did not suffer more from performing a 2-back task compared to a 1-back task ($F(1,17)=.891$, $p=.358$). The numerical decrease in capacity for fragile VSTM was indeed not much larger during the 2-back task compared to the 1-back task (.61 items versus .40 items respectively). Visual working memory capacity on the other hand showed a larger decrease when performing a 2-back task compared to a 1-back task ($F(1,17)=4.76$, $p=.043$), corresponding to a numerical difference of 2.29 versus 1.57 items respectively. We therefore suggest that a 2-back task has a larger effect on visual working memory than on fragile VSTM, but that the power of these experiments was too small to produce a significant three-way interaction.

In Experiment 2, the basic memory capacity scores on fragile VSTM were again rather high (1-back: K = 7.33; 2-back: K = 7.43). If a ceiling effect would be the explanation for the lack of an effect on fragile VSTM, this would result in a negative correlation between basic memory capacity score and decline in performance. However, there was absolutely no correlation between memory capacity score and decline in performance during the two dual-tasks (Fig. S2.2, 1-back: Pearson's R = .01, p = .968; 2-back: Pearson's R = -.06, p = .820). It is therefore unlikely that a ceiling effect could explain these results.

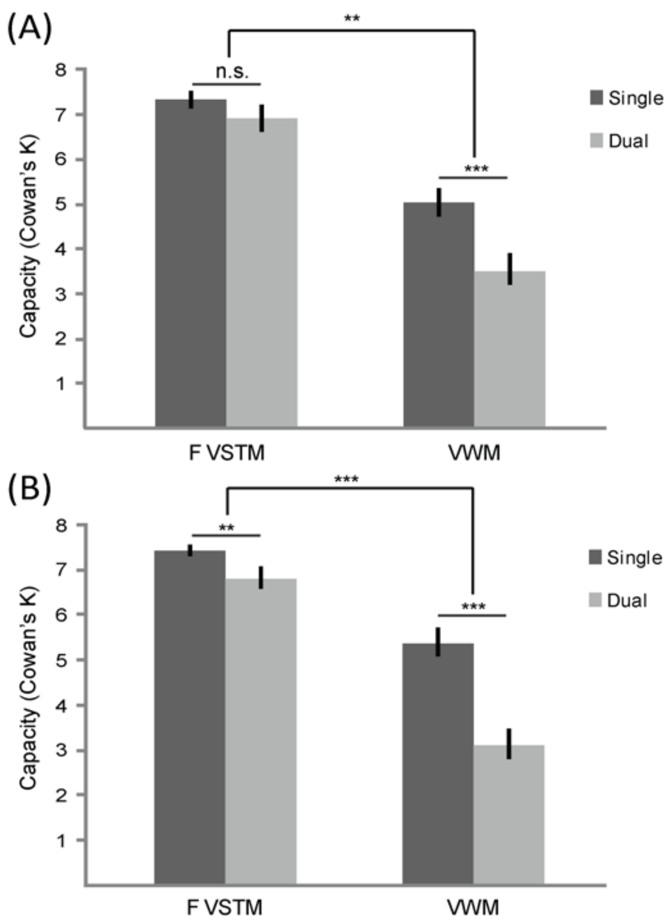

Figure 2.5. Experiment 2: Results. Performance on fragile VSTM (F VSTM) and visual working memory (VWM) trials expressed in capacity (Cowans's K). *A) Results for the 1-back session. There was a larger reduction for VWM than for F VSTM when subjects performed the two tasks simultaneously (dual) compared to the change detection task only (single). B) Results for the 2-back session. The same results were obtained as for the 1-back session. * p < .05, ** p < .01, *** p < .001*

Discussion

In this experiment, an n-back task was used to divert attention from the memory array. The results were congruent with the results of Experiment 1. When attention for the memory array was diminished, visual working memory suffered more than fragile VSTM. Moreover, when the secondary task became more attention demanding, visual working memory seemed to decrease even more, while the effect on fragile VSTM remained just about the same. We conclude that, because at the moment of encoding and maintenance subjects were engaged in an attention demanding secondary task, they had less attentional resources available to store the items in visual working memory. Fragile VSTM, however, was less affected, because this stage of memory is not dependent on attention.

Experiment 3

In the previous experiment, a dual task design was used to divert attention from the memory array. We assumed that because subjects focused on the n-back task, their attention for the memory array would be diminished. Although the n-back task is associated with activation of the prefrontal cortex (Owen, McMillan, Laird, & Bullmore, 2005) and thus likely to depend on attentional resources, we also wanted to employ an attention manipulation that is known to effectively decrease attention for a short period of time. The Attentional Blink (AB) paradigm seemed like a good candidate. In classical AB tasks, an RSVP stream of letters or characters is presented (Olivers et al., 2007; Raymond et al., 1992; Shapiro, 2009) participants have to detect two targets that are presented in this stream. When the second target (T2) is presented in close proximity of the first target (T1), T2 is less likely to be detected. This effect has been attributed to the momentary lack of availability of attentional resources; therefore the second target is not perceived. This lapse of attention has been shown to affect spatial processing (Olivers, 2004) and performing a secondary task, such as a visual search task, as well (Joseph, Chun, & Nakayama, 1997). Electrophysiological studies have shown that especially the P300 component, often associated with working memory, seems to be affected during the blink (Vogel & Luck, 2002). On the other hand, there is still some processing of T2 by lower level areas of the brain (Luck et al., 1996; Marois et al., 2004; Sergent et al., 2005), which can constitute semantic information.

For this experiment, we integrated the rectangle memory array in an AB task by presenting it as T2 in a character stream (Fig. 2.6). We expected that when the memory array was presented in proximity of T1, it would suffer from the AB. We hypothesized that during the AB, visual working memory would fail to come about because higher-level processes are suppressed. However, fragile VSTM that probably depends on activation of lower level areas would still be formed.

Methods

Subjects

Out of the 23 participants that passed the training, 18 took part in Experiment 3 (age 17 – 27). Of these 18 participants, 9 took part in Experiment 1 and 13 in Experiment 2 as well.

Stimuli and apparatus

Apparatus are described in *Stimuli and apparatus* of the General Methods. The memory and probe arrays in this experiment were modified such that the rectangles and background were now isoluminant (red on grey, both 24.65 cd/m2). This way, the memory array did not produce an afterimage. Compared to the attention manipulations used in the first 2 experiments, the AB was locked to a certain time window, so we wanted to make sure that in this task the image was present for just a short period of time. Otherwise, the configuration of the arrays was the same.

The stimuli used for the RSVP task were the same stimuli as used by Olivers et al. (2007). The targets were letters made of horizontal, vertical and diagonal line elements of a 2 X 3 grid square. The distracters used were scrambled letters; the line elements of the letters used as targets were scrambled into fantasy characters. The fantasy characters still looked a bit like letters because of certain constraints (e.g. the line elements must be connected). The letters I, L, O and Q and their corresponding distracters were taken out because they resembled each other or other letters too much. The letters were isoluminant with respect to their background as well (red on grey, 24.65 cd/m2).

Design and Procedure

A green fixation dot indicated the beginning of a trial. After 1000 ms, the fantasy characters appeared on the screen one after another (Fig. 2.6). Each character was presented for 66 ms with an ISI of 50 ms. In total, there were 11 or 13 fantasy characters in a stream (randomly distributed). Somewhere in this character stream, a letter was presented (T1). After this stream of characters the rectangle array was presented for 66 ms. Thus, the memory array was now the T2 target. After a 1000 ms blank interval, the cue was presented (retro or post-change) for 500 ms. Participants then first gave their response on the change detection task. When they had answered the change detection task, they answered which letter they had seen in the character stream by typing in the letter on a keyboard. T2 was positioned such that it was 2, 3, 4 or 8 lags back from T1. For each cue type, there were 32 trials per lag position (50 % change trials).

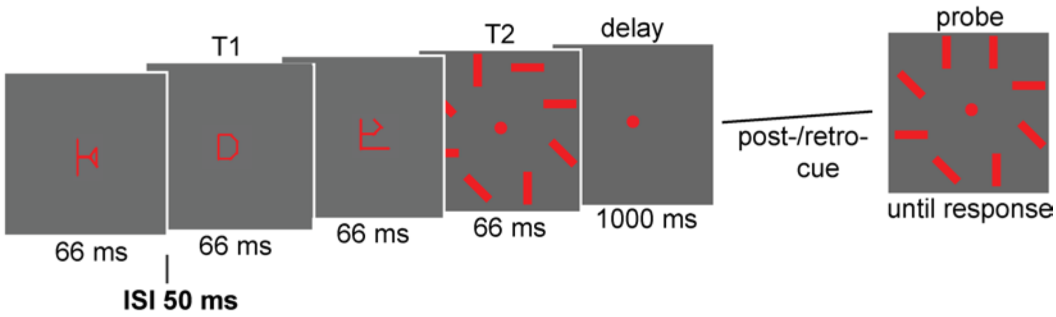

Figure 2.6. Experiment 3: Trial Design. The change detection task combined with an AB paradigm. *Preceding the memory array (T2), 12 or 14 characters were presented (Olivers et al., 2007), one of which was a real letter and the others were fantasy characters resembling letters. On each trial, subjects had to detect the letter (T1). The lag between T1 and T2 could be 2, 3, 4 or 8 (lag 2 is depicted). After the presentation of the memory array, the trial proceeded as a post- or retro-cue trial.*

Participants first received a practice block of the basic change detection task for 96 trials (48 retro-cue, 48 post-cue). The arrays were isoluminant and the memory array was only presented for 66 ms to get used to the presentation used in the AB-change detection task. Subjects then received three different tasks (counterbalanced). They performed the classical AB task, in which two letters were presented in the character stream. Their task was to first respond which was the second letter they had seen (T2) and then which was the first letter they had seen (T1). The character streams now consisted of 14 or 16 characters, because T2 was always followed by two more fantasy characters to mask it and make sure there was an AB effect (Enns, Visser, Kawahara, & Di Lollo, 2001; Vogel & Luck, 2002). Participants received 256 trials (64 trials per lag position) and first did a training session of 32 trials in which the stimulus time started at 100 ms and was decreased to 66 ms, while ISI started at 100 ms and was decreased to 50 ms. Participants received the combined AB-change detection task twice; once they had to respond to both T2 and T1 (16 practice trials, 256 experimental trials) to measure the effect of the AB on memory performance and once they only responded to T2 (16 practice trials, 256 trials). This last task served as the basic memory capacity score.

Analyses

For the basic AB task containing only the character stream, the AB effect was measured by calculating percentage correct for identifying T2 when T1 was answered correctly. If T1 is not answered correctly, there cannot be an AB, so these trials were not taken into the analyses. A repeated measure ANOVA on percentage correct for each lag (2,3,4,8) was performed.

As in Experiment 1 and 2, analysis for memory capacity was done with Cowan's K (see *Analyses* for Experiment 1). A repeated measures ANOVA was performed for memory type (fragile VSTM, visual working memory) X type of task (dual, single) X lag position of T2 (2,3,4,8). For the AB-change detection task in which participants responded to both T2 and T1, only the trials in which T1 was answered correctly were used in the analysis; if T1 is not answered correctly, there cannot be an AB, so these trials are not informative. The single task served as the basic memory capacity and because participants did not respond to T1, all trials per lag were used.

Results

For the basic AB task, there was a clear effect of lag ($F(3,15)=22.7$, $p<.001$). Identification of T2 was lowest when the lag between T2 and T1 was small (lag 2: 47.8 %) and gradually increased until the lag between T2 and T1 was large (lag 3: 61.4 %, lag 4: 75.6 %, lag 8: 85.5 %).

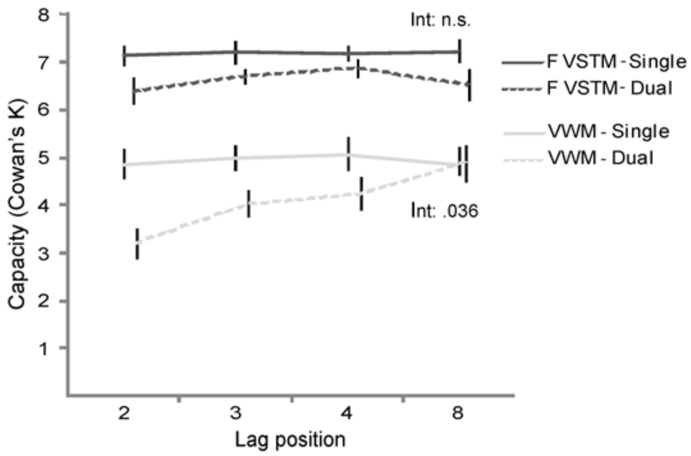

Figure 2.7. Experiment 3: Results. *Capacity for fragile VSTM (F VSTM, dark grey) and visual working memory (VWM, light grey) on the combined AB-change detection task (expressed as Cowan's K). On the single task, subjects only responded to T2 (solid lines). On the dual task, subjects responded to both T2 and T1. On the single task, performance for F VSTM and VWM was the same for each lag position of T2. When performing the dual task, F VSTM capacity showed a small general decrease, but VWM capacity showed a clear Attentional Blink: capacity decrease was largest for lag 2 and absent for lag 8. * p < .05, ** p < .01, *** p < .001*

Once again, a larger capacity for fragile VSTM versus visual working memory was found ($F(1,17)=157.2$, $p<.001$). Detecting T1 had a negative effect on memory performance in general ($F(1,17)=18.2$, $p=.001$) and performance on each lag position differed ($F(3,51) = 3.9$, $p=.014$).

Although the general decrease in performance was the same for both types of memory (fragile VSTM: 0.57 items, or 7.9 % reduction; visual working memory: 0.85 items, or 17.2 % reduction, $F(1,17)=1.0$, $p=.331$), there was a clearly different pattern for each lag ($F(3,51)=2.9$, $p=.042$). As can be seen in Figure 2.7, there was a general decline in performance for fragile VSTM, but the lag position of T2 did not affect memory performance differently. For visual working memory, however, a clear AB can be seen: when there is a small lag between T2 and T1, T2 performance shows the greatest decline, but performance recovers when the lag between T2 and T1 becomes larger.

Discussion

In the last experiment, the effect of attention on memory performance was once again demonstrated. When a change detection task was combined with an AB task such that the change detection memory array served as T2, visual working memory suffered from an AB, whereas fragile VSTM only showed a small general decrease in performance. Thus, the decrease in attention specifically affected visual working memory. In this experiment, the interaction effect was unlikely due to ceiling performance on the fragile VSTM trials, since the mean decrease in performance on both types of memory was equal. The effect of attention was marked by a different pattern for fragile VSTM and visual working memory and this pattern should not be absent due to ceiling.

Besides the fact that this experiment clearly dissociates between fragile VSTM and visual working memory, it replicates findings that the high capacity of fragile VSTM is not due to visible persistence (Sligte et al., 2008). The arrays used in this experiment were isoluminant and therefore did not produce an afterimage. Subjects were thus not able to rely on an afterimage to increase their performance.

General Discussion

In this study, we dissociated different stages of VSTM by manipulating attention during encoding of a memory array. Using a change detection task, we showed that fragile VSTM does not depend on attention, while visual working memory does. When a retro-cue was presented during the interval between the memory and probe array, almost all items could be retrieved even when attention was weakened during presentation of the memory array. In the post-cue condition, however, weakening attention during memory array presentation had a pronounced negative effect on memory capacity.

Albeit to a smaller extent, performance on the fragile VSTM task also suffered from the manipulations. However, this seemed more likely to be due to a general effect of performing a more difficult (Experiment 1) or dual task (Experiment 2, 3). Especially Experiment 3 showed that this effect was general and not due to the specific manipulation of attention. Another explanation might be that attention affected perceptual processing itself (Awh et al., 2006; Vogel et al., 2005). This would logically affect all levels of VSTM and might be a reason for the small general decrease in performance for fragile VSTM. On the other hand, one might expect that this effect would be time locked to the AB in Experiment 3 as well. Nevertheless, the key point here is the effect of attention on post-perceptual processing, and this seems to differentially affect fragile VSTM and visual working memory. The results clearly argue for viewing fragile VSTM as independent from visual working memory and attention. In combination with earlier results showing the difference between iconic memory and fragile VSTM, a tri-partite division of visual storage seems in order, comprising iconic memory, fragile VSTM and visual working memory respectively.

The interaction between VSTM and attention

The current results contribute to the debate about the involvement of attention in VSTM. Many have described that the two processes are closely linked and are supported by overlapping brain areas (Awh et al., 2006; Awh & Jonides, 2001; Cowan, 2001; Fougnie, 2008). It has even been proposed that attention is necessary for encoding and maintenance of VSTM. The present study, however, suggests that there are different stages in VSTM and that the role of attention in these stages can be clearly separated. At first, when a picture is shown, all items are represented for a very short period of time in a sensory store that is probably supported by lingering activity in lower visual areas (Irwin & Thomas, 2008). Fewer items are then maintained for a longer period of time in a fragile VSTM store supported by higher visual and inferotemporal areas (Sligte et al., 2009). Finally, only the few items that receive focused attention are represented in visual working memory mediated by frontal areas of the brain (Curtis & D'Esposito, 2003; Lepsien et al., 2005; Pessoa et al., 2002). The activity in these frontal areas probably boosts activity in the visual areas by means of feedback (Ranganath & D’Esposito, 2005). This protects these items from overwriting by new stimulation and makes them available for cognitive manipulation and report. The latter ability probably underlies what is mostly measured in classical VSTM or visual working memory tasks.

In the present study, we explicitly tried to address whether the contents of visual memory can be formed independently of attention. However, many scholars suggest that attention is especially important during the maintenance or rehearsal of visual working memory (Awh et al., 2006; Awh & Jonides, 2001; Cowan, 2001). We predict that reducing attention during maintenance would have the same effect as reducing attention during encoding: visual working memory capacity decreases, but fragile VSTM remains intact. Although we did not test this explicitly, previous research has shown that items can still be accessed even after attention has been directed to one item in the display (Landman et al., 2003). In this study, two consecutive retro-cues are shown on 25 % of the trials, and only the second cue is valid. The second cue can still boost memory up to a higher performance level than without a retro-cue. It thus seems that representations in fragile VSTM still remain available for report, even when another item has been attentionally selected for maintenance.

The distinction between memory storage and attention also coincides with the ideas of Postle (2006) that the prefrontal cortex plays a controlling and mediating role and is not the locus for storage of information content. We demonstrate that when the prefrontal cortex is engaged in another task, the controlling and mediating role on VSTM is diminished, but the storage of information is unaffected. Another recent study from our lab further supports these results by showing that when TMS is applied on the right DLPFC, visual working memory is impaired while fragile VSTM stays intact (Sligte et al., 2011).

The attention manipulations

Attention was manipulated in three different ways. In the first experiment, subjects had to pay attention to multiple arrays, because they were uncertain when the memory array would appear. We hypothesized that subjects were not able to adequately allocate their attention to the memory array (Coull et al., 2000; Nobre, 2001; Small et al., 2003). Although the manipulation had a larger effect on visual working memory than on fragile VSTM, an alternative explanation is that clearing memory takes time or happens in an imperfect way. This would then have a larger effect on working memory (having a smaller capacity) than on fragile VSTM (having a larger capacity). To make sure that the difference in performance was attention-related, we also wanted to employ a more central attention manipulation. We therefore conducted two more experiments in which attention was decreased by presenting subjects with a dual-task setting.

In the third experiment, we used an Attentional Blink paradigm to diminish attention for the memory array. This is a well-known attention manipulation that has a selective effect on attention. We do not want to make any statements about the AB itself. It could be debated whether an AB can be found for two different types of stimuli. However, Olivers (2004) showed that spatial processing is affected by the AB and Jospeh et al. (1997) demonstrated that a secondary task is affected by detecting a first target. Another important issue is the necessity of presenting a mask after T2 (Enns et al., 2001; Vogel & Luck, 2002). In our design, this was not possible, as the fragile VSTM traces would be immediately overwritten by the presentation of similar visual stimulation. On the other hand, this exactly could be the reason why in classical AB paradigms, a mask is needed to induce an AB: if there is no mask, T2 can be recovered from fragile VSTM (Luck et al., 1996; Vogel & Luck, 2002).

High memory capacities

Our data raise two important concerns regarding the memory capacity scores. First, visual working memory capacity is higher – about one object - than usually measured in visual working memory tasks. One explanation is that subjects received extensive training for the task and only those that performed sufficiently were allowed to participate in the experiments. Hence, the subject pool had a high average visual working memory capacity. Moreover, as the experiments progressed, subjects that participated in multiple experiments were exposed to the task even more. This probably led to a boost in the average memory capacity. However, the main focus of this study is not memory capacity per se, but rather that visual working memory suffers more from reduced attention than fragile VSTM does.

The second concern is that attention manipulations could have had less effect on fragile VSTM because of a possible ceiling effect. However, correlations between basic performance and the drop in performance were not significant. This means that the drop in performance was the same for subjects with a high or a low capacity, hence the interaction effect was probably not driven by ceiling performance.

VSTM, attention and consciousness

Our results are not only relevant to the debate on VSTM, but can also be viewed in relation to theories on consciousness. The outcome shows that conscious memory representations can arise independently of attention, which is in accordance with theories proposed by Block (2005, 2007) and Lamme (2006, 2010). According to these authors, consciousness arises as a result of recurrent processing, while attention is dependent on the depth of processing, i.e. whether frontal regions are involved or not. The prediction is that when recurrent processing is local, and thus unattended, the representations are conscious, but not yet available for report. Only when recurrent processing has spread to frontal regions, involving attention, the representations can be reported about. Our study supports this model by showing that memory traces can be formed independent of attention. When the memory has to be reported about however, attention has to be directed to the memory. This suggests that consciousness itself does not depend on attention, but is manifested by it behaviorally.

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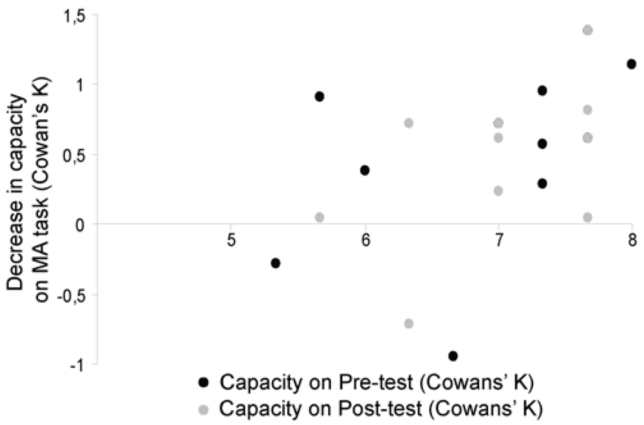
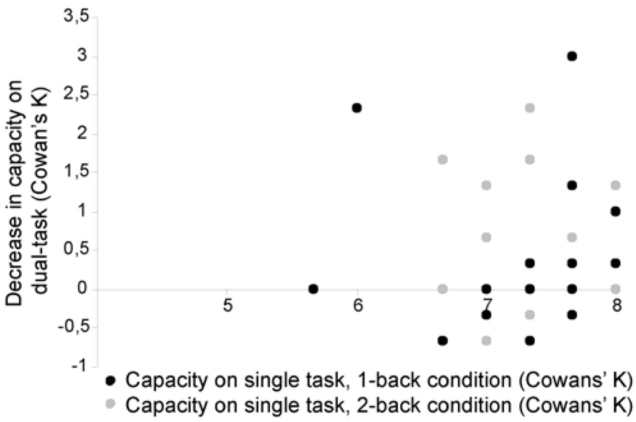
Supplementary Figures



Supplementary Figure 2.1. Experiment 1: Correlations between tasks for fragile VSTM performance. *Correlation between fragile VSTM (F VSTM) capacity on the pre-test and its decrease during the Multiple Array (MA) task (black dots, R = .326) and F VSTM capacity on the post-test and decrease during MA task (grey dots, R = .245). There is no relation between capacity on the single task and decline in capacity on the MA task. This suggests that the relatively small decrease during the MA-task is not due to ceiling performance; if ceiling performance would drive these results, this would result in a small decline for high-capacity individuals and a large decline for low-capacity individuals.*



Supplementary Figure 2.2: Experiment 2: Correlations between tasks for fragile VSTM performance. *Correlation between fragile VSTM (F VSTM) capacity on the single-task and its decrease during the dual task for the 1-back session (black dots, R = .01) and the 2-back session (grey dots, R = -.06). There is no relation between capacity on the single task and decline in capacity on the dual task. This suggest that the relatively small decrease during the dual tasks is not due to ceiling performance; if ceiling performance would drive these results, this would result in a small decline for high-capacity individuals and a large decline for low-capacity individuals.*