A new definition of visual short-term memory
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6. Brain anatomy constrains the capacity of sensory memory and working memory

Brains are organized in a clear hierarchical fashion, with sensory areas at the bottom and control and motor areas at the top of the hierarchy. At each subsequent level in this hierarchy, progressively less information can be processed simultaneously. This same principle is evident in different forms of visual short-term memory (VSTM): people maintain many representations in sensory memory, but only 3-4 representations in visual working memory. Here, we show for the first time a relation between the capacity of different forms of VSTM and brain anatomy. Specifically, we found significant correlations between 1) the size of early sensory areas and iconic memory capacity, 2) the size of extrastriate visual areas and the capacity of fragile visual short-term memory, and 3) the size of parietal and frontal areas and visual working memory capacity. Thus, it seems that an individual’s information processing capacity is related to the size of his/her brain, albeit at different levels in the neural hierarchy for different forms of VSTM.

**Introduction**

To guide our behavior in successful ways, we often need to rely on information that is no longer in view, but maintained in visual short-term memory (VSTM). Usually, VSTM is dissociated into iconic memory, a brief and high-capacity store operating close to perception (Neisser, 1967; Sperling, 1960), and visual working memory, a sustained and capacity-limited store operating at the interface of perception and action (Luck & Vogel, 1997). Recent studies, however, have shown the existence of a third and fragile form of VSTM that operates between iconic memory and visual working memory (Griffin & Nobre, 2003; Landman, et al., 2003; R. Landman, et al., 2004; Lepsien, et al., 2005; Lepsien & Nobre, 2007; Makovski & Jiang, 2007; Makovski, et al., 2008; Matsukura, et al., 2007; Sligte, et al., 2008); it has a much higher capacity than working memory and at the same time a lifetime that is a factor 10 longer than the lifetime of iconic memory (Landman, et al., 2003; Lepsien & Nobre, 2007; Sligte, et al., 2008). Moreover, this fragile form of VSTM resides in extrastriate visual cortex (V4) (Sligte, et al., 2009), while iconic memory depends on activity lower in the neural hierarchy (Maunsell & Gibson, 1992) and working memory on activity higher in the neural hierarchy (frontal and parietal regions) (Courtney, Petit, Maisog, Ungerleider, & Haxby, 1998; Linden, et al., 2003; Pessoa, et al., 2002; Todd & Marois, 2004). Thus, it seems that short-term memory processes form a continuum with brief lifetimes, high capacity and basic processing low in the neural hierarchy and long lifetimes, low-capacity and deep processing high up in the neural hierarchy.

While it is evident that capacity bottlenecks become stricter as we progress from iconic memory to visual working memory, it is not well understood how capacity bottlenecks are implemented in the brain. The only starting point comes from a number of functional studies (Mcnab & Klingberg, 2008; Todd & Marois, 2004; Vogel & Machizawa, 2004; Xu & Chun, 2006) showing a link between brain activity in parietal and frontal cortex and individual differences in visual working memory capacity. Here, we aim to show that a general principle underlies capacity bottlenecks in all forms of VSTM; specifically, grey matter density (or brain size) is tightly linked to information processing bottlenecks, albeit at different levels in the neural hierarchy for different forms of VSTM.

To anticipate, we show in this paper a clear link between grey matter density and the capacity of different stages in VSTM. At the lowest cortical level in the neural hierarchy (primary sensory areas), grey matter density seemed to constrain the capacity of iconic memory. The capacity of fragile VSTM was related to grey matter density at a slightly higher cortical level in the neural hierarchy (extrastriate visual cortex); the location of this brain region more or less corresponds to the location where neural activity related to fragile VSTM
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was found recently (Sligte, et al., 2008). Finally, at the highest levels in the neural hierarchy (frontal and parietal cortex), grey matter density was related to visual working memory capacity. Thus, it seems that brain size limits the amount of information people can process concurrently, and these anatomical bottlenecks are evident at multiple levels in the neural hierarchy.

Methods

Subjects

58 adults participated in this experiment for course credits or financial compensation. All subjects gave their written informed consent to participate in the study, which was approved by the local ethics committee of the department of Psychology of the University of Amsterdam. Six subjects were excluded from the analyses as they performed two standard deviations below the mean performance, averaged across all conditions (note that the overall pattern of results did not change when including these subjects).

Experimental paradigm

Stimuli were presented with Presentation (Neurobehavioral Systems) on a 17-inch VGA-monitor. Stimulus displays consisted of 8 white oriented rectangles (87.66 cd/m²) that were each 1.56° × 0.39° in size and these rectangles were placed equidistantly on a black background (0.01 cd/m²) at an eccentricity of 5° of visual angle surrounding a red fixation dot (0.48° diameter, 13.52 cd/m²). The orientation of each rectangle could be horizontal, vertical, 45° to the vertical, or 135° to the vertical and each orientation was present at least once in the display and at most three times. This last manipulation was to done to prevent grouping of the individual items, although previous work using oriented rectangles has shown that grouping effects of these stimuli are negligible (Sligte, et al., 2008). Cues were composed of three-pixel thick lines that were on one side close to the fixation dot (distance 0.7° of visual angle) and at the other end close to the centre of one rectangle (1.2° of visual angle). See Figure 6.1 for examples of the displays used.

On each trial, the fixation dot in the centre of the display turned green for 1s to indicate the start of the trial. Then, a 250-ms memory display was shown that contained eight oriented rectangles and subjects were instructed to remember the orientation of each rectangle to their best ability. After offset of the memory display, a blank retention interval was shown either for 2s when cues were shown during maintenance or for 900 ms when the cue was shown after maintenance. After the blank retention interval, a test display was shown that was identical to the memory display in 50 percent of the trials. In the other 50
percent of the trials, all items were identical between memory and test display except for one rectangle that had switched to an orthogonal orientation. On each trial, subjects indicated by button press whether both displays were the same or whether one item had changed between displays. The test display was shown for 4s or until the subject made a response.

Figure 6.1 Experimental design Subjects were asked to memorize the orientations of eight rectangles across a retention interval. In 50 percent of the trials, the cued rectangle changed to an orthogonal orientation after the retention interval. On each trial, subjects made a forced-choice response whether there was a change or not. A. The attention-directing cue was presented 10 ms after offset of the memorized display and this condition measures iconic memory. B. The attention-directing cue was presented 1,000 ms after offset of the memorized display. Iconic memory is gone at this cue latency, but people can still access a high-capacity form of visual short-term memory that we termed fragile visual short-term memory previously. C. The attention-directing cue was presented after the change had already occurred. People show a clear capacity limit in this condition reflecting the limited capacity of visual working memory.

A crucial part of the experiment is the delivery of a 500-ms spatial cue that singles out the item to change. Previously, we found that when this cue is shown 10 ms after offset of the memorized display (Fig. 6.1A), people could report 30 (out of 32) items when the memorized display contained high-contrast stimuli, but only 20 (out of 32) when the display contained isoluminant stimuli (Sligte, et al., 2008). This suggests that retinal afterimages are driving iconic memory performance just after stimulus offset. Note that we did measure phosphor persistence of the display and there was absolutely no physical trace of the stimulus left onscreen 6.4 ms after stimulus offset. When the same cue was presented 1,000 ms after offset of the memorized display, but before onset of the test display (Fig. 6.1B), we observed that people could report a maximum of 15 (out of 32) items. Importantly, at this latency (> 1s after stimulus offset), iconic memory traces are long gone. We indeed found no differences in
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performance between high-contrast and isoluminant stimuli at this cue latency indicating that this high-capacity form of VSTM is not a form of iconic memory performance. In addition, features are bound to form coherent objects in this form of VSTM (Landman, et al., 2003), which is another distinction from iconic memory. We termed this memory store fragile VSTM as this form of memory is readily overwitten by new stimuli, yet its traces last up to four seconds when no new stimulus is shown (Lepsien & Nobre, 2007; Sligte, et al., 2008, 2009). Finally, when the cue was presented after onset of the test display, so after the potential change has occurred (Fig. 6.1C), people could report a maximum of four items regardless of set size and this corresponds to the well-known capacity limit of visual working memory (Luck & Vogel, 1997).

Behavioral data analyses
The behavioral performance of the subjects on the short-term memory tasks is reported as Cowan’s K (Cowan, 2001). In simplified form, this formula is $K = \text{set size} \times (\text{correct rejection rate on no-change trials} + \text{hit rate on change trials} - 1)$. This formula gives a conservative estimate of representational capacity that corrects for guessing.

VBM data acquisition and analyses
Magnetic resonance imaging (MRI) data were acquired from a Philips 3T scanner. For each individual, we acquired two high-resolution, anatomical MRI scans with conventional parameters (T1 turbo field echo; 182 sagittal slices; flip angle (FA) of 8°; echo time (TE) of 4.6 ms; repetition time (TR) of 9.6 s; slice thickness of 1.2 mm; field of view (FOV), 250 × 250 mm; in-plane voxel resolution, 0.98 × 0.98 mm). Data were analyzed with voxel-based morphometry (Good, et al., 2001) carried out with FSL software (S. M. Smith, et al., 2004). First, we extracted the brain from the structural image (S. M. Smith, 2002). Next, we performed tissue-type segmentation using FAST4 (Zhang, Brady, & Smith, 2001). The resulting grey-matter partial volume images were aligned to MNI152 standard space using the affine registration. The aligned images were then averaged to create a study-specific template, to which the native T1 images were non-linearly re-registered (Rueckert, et al., 1999); this method uses a b-spline representation of the registration warp field. We modulated the registered partial volume images to correct for local expansion or contraction by dividing by the Jacobian of the warp field (Ashburner & Friston, 2000). Finally, we applied an isotropic Gaussian kernel with a sigma of 4 mm to these modulated images. This procedure was applied independently to the first and second MRI image acquired from each
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subject. We will refer to the end product of these analyses as the first and the second “VBM image” in the rest of the paper.

To derive correlations between behavioral measures and brain structure, we performed a voxel-wise GLM analysis using permutation-based non-parametric testing (10,000 iterations) on the first (!) VBM image. Performance on all three visual short-term memory tasks was entered as covariates. We specified one contrast for positive and one for negative correlations for each condition (six contrasts in total). We selected clusters of 100 contiguous voxels that showed a statistical significance of \( p < .01 \) on either one of the contrasts. To ensure that selection and statistical testing were independent, we selected clusters based on the first VBM image and exported grey matter density values corresponding to the same stereotactic location from the second VBM image. We correlated these clusters again with behavior (Pearson’s \( r \)). In the end, out of the 25 exported clusters, 11 clusters still had a significance of \( p < .05 \), corrected for multiple comparisons (false discovery rate .017). Clusters showing a significance of \( p < .01 \) are shown graphically in the paper. All details on the clusters can be found in Table 6.1.

The stereotactic location of each significant cluster is reported as FSL-MNI standard space. The corresponding Brodmann area was determined with the Talairach atlas that is implemented in FSLview.

Procedure

In the first session, we screened participants on whether it was safe to put them into the MR scanner. After successful screening, subjects practiced the task (early retro-cue/late retro-cue/post-change cue) for about 10 minutes (30 trials in each condition) and all conditions were randomly intermixed. Then, they performed the actual experiment for about 20 minutes (60 trials in each condition) and again all trials were randomly intermixed. After the experiment, the participants were debriefed about the goal of the study. In the second session, each participant was put into the MR scanner and we acquired two high-resolution T1 images.

Results

To probe capacity bottlenecks in VSTM, 52 subjects performed a modified change detection task that measures iconic memory (Fig. 6.1A), fragile VSTM (Fig. 6.1B) and visual working memory (Fig. 6.1C) in a single experiment. For an exact description of the task and the reasons why these different conditions measure three different forms of VSTM, we refer to the Materials and Methods section and previous work of our lab (Sligte, et al., 2008). We
found that people on average could maintain 7.0 objects in iconic memory, 5.7 objects in fragile VSTM and 2.9 objects in visual working memory (see Fig. 6.2; left-side of graph). Capacity differences between stores were all highly significant (lowest value: \( t(51) = 7.17, p < .001 \)). Moreover, the actual capacity of each form of VSTM differed strongly between individuals, reflecting how much information a person can process concurrently at different levels in the information processing hierarchy (see Fig. 6.2; right-side of graph); iconic memory capacity ranged from 4.8 to 8.0 objects, fragile VSTM capacity from 2.7 to 8.0 objects, and visual working memory capacity from 0.5 to 5.9 objects.

*Figure 6.2 Behavioral performance* Iconic memory performance is shown in blue, fragile visual short-term memory performance in red and visual working memory performance in green. On the left side of the graph, the mean performance for all forms of visual short-term memory is displayed. The size of the circles represents the standard error of the mean and the dotted circles represent the standard deviation. On the right side of the graph, the distribution in performance of all subjects is shown. Performance is expressed as Cowan’s K (Cowan, 2001).

We correlated single-subject performance on these three different memory stores with voxel-based morphometry (VBM) measures. VBM gives an estimate of the amount of grey matter in particular brain areas relative to the surrounding areas. In this between-subjects design, higher VBM values can either be ascribed to a larger brain area or to more grey matter (more neurons/more dendrites) in a brain area that has the same volume. To ensure that selection and statistical testing were independent, we acquired two anatomical high-resolution volumes that were both transformed into VBM images (see Materials and Methods). We selected significant clusters (\( p < .01 \) for 100 contiguous voxels) based on non-parametric correlations between behavior and the first VBM image, resulting in 25 clusters. We extracted these clusters from the second VBM image and only clusters that still showed a significant correlation with behavior, corrected for multiple comparisons (false discovery rate of .017), are reported. This entire procedure gives a conservative and unbiased estimate of
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brain regions that are correlated with visual short-term memory (Kriegeskorte, Simmons, Bellgowan, & Baker, 2009).

We found that individuals with a higher iconic memory capacity had a larger right visual cortex (Fig. 6.3A; BA17/18; \( r = .37, p = .003 \)) and a smaller right auditory cortex (Fig. 3A; BA 41/42: \( r = -.48, p < .001 \)). This suggests that the representational capacity limit of iconic memory is set by grey matter volume in primary sensory areas and these areas together explained 27.1 percent of the variance in iconic memory capacity. Speculatively, from the inverse relation between auditory and visual cortex volume in relation to the capacity of iconic memory, it seems that some people have a more visual neural architecture, whereas others (those with low iconic memory) have an auditory preference.

The capacity of fragile VSTM was higher in individuals with a larger right extrastriate cortex (Fig. 6.3B; BA 19; \( r = .43, p = .001 \)); an area that roughly corresponds to visual areas V4 and posterior inferotemporal cortex (IT). Additionally, we found a positive correlation between the left supplementary motor area (SMA) and fragile VSTM capacity (Fig. 3B; BA 6; \( r = .36, p = .004 \)). Together, these areas explained 26.9 percent of the variance in fragile VSTM capacity. Previously, we found that neural activity in visual area V4 is related to maintenance of fragile VSTM (Sligte, et al., 2009). Here, we show that anatomical differences in that same area explain individual differences in the representational capacity of fragile VSTM. Thus, it seems that extrastriate visual areas maintain a high-capacity representation of the outside world that is evident in both functional and anatomical data.

Finally, the capacity of visual working memory was higher in individuals with a smaller right pre-SMA/SMA (Fig. 6.3C; BA 6; \( r = -.41, p = .001 \)), a larger right premotor cortex (Fig. 3C; BA6; \( r = .45, p < .001 \)) and a smaller right precuneus (Fig. 6.3C; BA 7; \( r = -.46, p < .001 \)). In addition, we found multiple negative correlations with clusters in frontal and medial temporal cortex (see Table 6.1). Together, these areas could explain 55.5 percent \( (r^2) \) of the variance in visual working memory capacity. We note that the high-level areas that impose capacity limits on visual working memory are those that are involved in the default network (right precuneus) (Raichle, et al., 2001), rehearsal of spatial and non-spatial information (right premotor cortex) (Courtney, et al., 1998; Owen, Evans, & Petrides, 1996), and resolution of conflict when multiple alternatives are present (right pre-SMA) (Nachev, Kennard, & Husain, 2008).
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Figure 6.3 There are large individual differences in the capacity of iconic memory, fragile VSTM and visual working memory. Here, we correlated grey matter density of our participants with their performance on three different visual short-term memory tasks. Note that left-handed clusters are in the left hemisphere and vice versa. Statistical values reported are one-sided. A. Individuals with high-capacity iconic memory had more grey matter volume in the right visual cortex and less grey matter volume in the right auditory cortex. B. Individuals with high-capacity fragile visual short-term memory had more grey matter volume in the left supplementary motor area and in an area roughly corresponding to visual area V4 and the posterior part of the inferotemporal cortex. C. Individuals with high-capacity visual working memory had more grey matter volume in the right premotor cortex and less grey matter volume in the right pre-supplementary motor area and the right precuneus.

Discussion
The three different memory stages we investigated have increasingly stricter capacity limits and a progressively higher-level cognitive signature. Therefore, one would expect to see that capacity limits are imposed at a low level in the neural architecture for iconic memory, at an intermediate level for fragile VSTM and at a high level for visual working memory. This is exactly what we found. Bottlenecks in capacity are imposed by the anatomy of early sensory areas for iconic memory, by extrastriate visual areas for fragile VSTM, and by high-level
brain areas that play a role in higher-order cognitive processing for visual working memory. In sum, it seems that people's information processing capacities are determined by the size of their brain at several levels in the neural hierarchy.

The relation between grey matter density and VSTM capacity

One of the first questions that pops into mind is what is causing these anatomical differences. Are they caused by genetics or years of practice and brain plasticity? In general, brain characteristics such as brain volume (Baare, et al., 2001), grey matter density (Thompson, et al., 2001) and brain connectivity (Brun, et al., 2009) are heritable, suggesting that the current finding can in part be attributed to genetics. However, when people learn a new ability, such as juggling (Draganski, et al., 2004), mirror reading (Ilg, et al., 2008), and extensive studying (Draganski, et al., 2006), this can readily be observed in grey matter changes within a few weeks. As VSTM processes are core business in our everyday life, it may be that the anatomical differences found here are (partially) the result of years of everyday practice.

Still, this does not tell us anything about the mechanism of how denser brain areas enable higher VSTM capacities. As explained earlier, higher voxel-based morphometry (VBM) values indicate that a particular brain area is either relatively large in volume, or relatively dense in the number of neurons and dendrites compared to surrounding brain areas. It is plausible that more calculating units (neurons) in a specific brain area and/or more densely connected units can both support higher capacities. However, these explanations are highly speculative as there are still many unknowns about what VBM is exactly measuring.

Right hemisphere specialization for VSTM processes?

While it is plausible to find a relation between iconic memory capacity and the visual cortex, and between fragile VSTM capacity and the extrastriate cortex, it is not obvious why this is only evident for the right hemisphere. Such an asymmetry is not completely illogical as most working memory studies do show a similar asymmetry, in the sense that verbal information is more strongly represented by the left hemisphere and visual information more strongly by the right hemisphere (Baddeley, 2003; Jonides, et al., 2008; Wager & Smith, 2003). This verbal-visual asymmetry is typically more prominent in the frontal cortex than in posterior parts of the brain, yet it might be that our analyses selectively picked up on the more subtle posterior asymmetries.
Considerations about working memory-related anatomical differences

Only parts of the pattern related to working memory capacity match the typical patterns of activations found in several fMRI studies (Courtney, et al., 1998; Courtney, et al., 1997; Pessoa, et al., 2002; E. E. Smith & Jonides, 1998). Most notably, the intraparietal sulcus and the middle frontal gyrus are missing (Linden, et al., 2003; Todd & Marois, 2004). In our initial analyses, we did observe small clusters in the right intraparietal sulcus and the bilateral middle frontal gyrus that were correlated with working memory capacity. However, these clusters were not robust enough to survive the test-retest procedure we used to ensure that data selection and statistical analysis were independent. It is likely that there was too much variance in the exact location of the intraparietal sulcus and the middle frontal gyrus between subjects to show up in our final analyses.

Another important finding to address is the observation of multiple negative correlations between visual working memory capacity and VBM: why does working memory capacity suffer when specific brain areas are bigger? The most plausible explanation is that people use different strategies to maintain information in working memory (McNamara & Scott, 2001). These different strategies are very likely to depend on different brain areas. Thus, low-capacity individuals may recruit other networks than high-capacity individuals for working memory maintenance, resulting in negative correlations between working memory capacity and the size of these other brain regions. In addition, we need to consider that different psychological factors are important for working memory maintenance: for instance, concentration span (or the lack of distractibility) is just as important for high working memory capacity as the ability to attend to multiple spatial locations at the same time (Sauseng, et al., 2009; Vogel, McCollough, & Machizawa, 2005). If distractibility is related to the size of particular brain areas, this may in turn cause negative correlations between VBM and working memory capacity.

A potential link between brain anatomy and brain activity?

As capacity limits in VSTM are evident both in anatomy and in functional measures of the living brain, one might question whether individual differences in anatomy give rise to differences in brain activity. There are two hints in the present paper that this might be the case. We found that individuals with higher fragile VSTM capacity had a larger extrastriate visual cortex. This region is in the vicinity of the visual area V4, where we previously found a neural correlate of fragile VSTM with the use of functional MRI (Sligte, et al., 2009). In addition, visual working memory capacity was related to the size of a cluster in the right premotor cortex and this same area is active during visual working memory maintenance.
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(Courtney, et al., 1998; Owen, et al., 1996). Hopefully, future studies will directly compare individual differences in grey matter density with individual differences in functional activity to reveal this potential link between brain anatomy and brain activity.

<table>
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<td></td>
<td>x     y     z</td>
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Table 6.1 All clusters showing a significant correlation with either form of visual short-term memory corrected for multiple (25) comparisons (false discovery rate = .017). Only clusters with \( p < .01 \) (two-sided) are shown graphically in the paper.