A new definition of visual short-term memory
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7. Summary and Discussion

"Memory is, therefore, neither Perception nor Conception, but a state or affection of one of these, conditioned by a lapse of time." Translated from On Memory and Reminiscence by Aristotle (350 BC).

Thus, a long, long time ago, Aristotle already suggested the existence of two forms of memory; one that operates close to perception and another that operates close to cognition. When considering visual short-term memory (VSTM), this distinction is evident in iconic memory (brief and high-capacity) and visual working memory (sustained, but low-capacity), respectively (Averbach & Sperling, 1961; Luck & Vogel, 1997; Pashler, 1988; Phillips, 1974; Sperling, 1960). Nonetheless, I discovered that this two-partite distinction of VSTM into iconic memory and visual working memory is too simplistic. Instead, we should discern at least three stages in VSTM and I termed them iconic memory, fragile VSTM and visual working memory respectively. Below, I will summarize the evidence for this tri-partite division of VSTM.

**Summary of the results: three stages in visual short-term memory**

In all studies reported in this dissertation, I have combined partial-report, iconic memory paradigms with change-detection, visual working memory paradigms. Depending on when the partial-report cue was presented during the change-detection task (see Fig. 7.1), I observed dramatically different behavior, which implied the existence of at least three different stages in VSTM. Moreover, these three different VSTM stages were associated with brain activity and/or brain structure at progressively higher levels in the brain hierarchy. In the following sections of this summary, I will report about the behavioral characteristics and neural basis of iconic memory, fragile VSTM and visual working memory.

**Iconic memory**

When a partial-report cue was presented just after offset of the memorized display (Fig. 7.1A; early retro-cue), people could report almost all objects (30 out 32 objects) that were present in the memory display provided that the memorized items were white objects on a black background (Chapter 2; Sligte, Scholte, & Lamme, 2008). When objects were red on a
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grey background of the same light intensity, people could report only 20 objects (out of 32 objects). This observation can be explained by the fact that high-contrast stimuli (white on black background) are “seen” by the rods in the retina, while isoluminant stimuli (red on grey background) are “seen” by cones only. As rod responses last significantly longer than stimulus duration, while cone responses do not (Adelson, 1978), it is as if the high-contrast stimulus is still on screen when the early retro-cue is presented and the task becomes very easy. Moreover, when a flash of light was presented just before the early retro-cue, we observed no superior performance anymore for high-contrast stimuli: the flash of light resets the rod responses and dramatically reduced the capacity of iconic memory. From these data, we might conclude that iconic memory is some kind of retinal after-effect after stimulus offset.

Figure 7.1 In the general set-up of this change detection task, people have maintain the identity of multiple objects in short-term memory across a retention interval. After the retention interval, one of the objects might change and people have to detect this potential change. On each trial, a cue is shown that singles out the item that might change. This cue is presented either A. 10 ms after offset of the memorized display (early retro-cue condition), B. 1000 ms after offset of the memorized display (late retro-cue condition), or C. 100 ms after onset of the test display, so after the potential change (post-change cue condition). These different cue conditions measure different stages of visual short-term memory: iconic memory, fragile visual short-term memory and visual working memory, respectively.

In a subsequent study (Chapter 3), we investigated the amount of visual detail or resolution of iconic memory (and of fragile VSTM and visual working memory). We found that the majority of iconic memory representations were visually detailed or high-resolution representations. Also, fragile VSTM representations were mostly high-resolution representations. However, visual working memory seemed to contain only one high-resolution object representation in addition to one low-resolution representation. Thus,
representations (constituting iconic memory and fragile VSTM) seem to be numerous and rich in visual detail before visual interference, but after visual interference capacity and resolution of VSTM is limited (constituting visual working memory).

Finally, we observed that people with high iconic memory capacity had a larger primary visual cortex and a smaller primary auditory cortex (Chapter 6). This implies that iconic memory is not just the passive firing of the retina beyond stimulus duration as suggested before (Chapter 2; Sligte et al., 2008). Instead, the anatomy at a low level in the neural hierarchy determines the amount of low-level visual information that can be processed simultaneously. Thus, iconic memory is related to a retinal after-effect just after stimulus offset that drives neural processes in primary visual cortex. This might explain why representations in iconic memory are rich in visual detail and why the capacity of iconic memory is so high.

**Fragile visual short-term memory**

When the partial-report cue was presented one second after offset of the memory display (Fig. 7.1B), people could report 15 out of 32 objects (Chapter 2; Sligte, Scholte, & Lamme, 2008). This is surprising as it is generally agreed that iconic memory lasts only half a second (Averbach & Sperling, 1961; Sperling, 1960), and that at longer delays performance has to rely on visual working memory that has a maximum capacity of four objects (Luck & Vogel, 1997; Vogel, et al., 2001). Yet, even when the late retro-cue was presented four seconds after stimulus offset, people still had access to more information than could fit in their visual working memory (Chapter 2; Sligte et al., 2008). To rule out that this high-capacity and relatively long-lasting memory store (from now on termed fragile visual short-term memory; VSTM) was a reflection of either iconic memory or visual working memory, we performed a series of experiments.

From our initial experiments, it was evident that fragile VSTM was not some kind of iconic memory as 1) differences in stimulus contrast had no influence on fragile VSTM capacity, but a profound effect on iconic memory capacity (Chapter 2; Sligte et al., 2008), 2) the presence of light flashes (Chapter 2; Sligte et al., 2008) or homogeneous textures (Landman, Spekreijse, & Lamme; 2003, 2004) during retention erased iconic memory, but did not affect fragile VSTM capacity, and 3) features were bound into coherent objects, a characteristic that has never been observed in relation to iconic memory (Landman et al.; 2003, 2004). Moreover, maintenance of fragile VSTM was related to activity in visual area V4 (Chapter 5), and an individual’s capacity was related to the anatomical size of his/her extrastriate cortex near area V4 (Chapter 6). In contrast, the capacity of iconic memory was
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related to the size of an individual’s primary visual cortex, which is at a lower level in the neural hierarchy. Thus, based on behavioral and neuroimaging results we can dissociate fragile VSTM from iconic memory.

Fragile VSTM neither seems to qualify as some kind of high capacity form of working memory as the presence of new objects before the late retro-cue completely erased fragile VSTM (Chapter 2; Sligte et al., 2008), while working memory is known to be resistant to overwriting. In addition, the amount of visual detail in fragile VSTM exceeded the detail of working memory representations (Chapter 3). However, the strongest argument was provided by a study (Chapter 4) in which we delivered transcranial magnetic stimulation (TMS) to the right dorsolateral prefrontal cortex (DLPFC), which is known to be involved with working memory maintenance. TMS caused clear decrements in performance on post-change cue trials measuring visual working memory, but not on late retro-cue trials measuring fragile VSTM. This implies that working memory representations recruit areas in the frontal cortex, whereas representations in fragile VSTM are confined to areas in posterior parts of the brain as both functional MRI (Chapter 5; Sligte, Scholte, & Lamme, 2009) and structural measures (Chapter 6) have shown. Altogether, these studies imply that fragile VSTM is a separate short-term memory store that operates in between iconic memory and visual working memory.

Visual working memory

Finally, when the partial-report cue was presented after maintenance, just after onset of the test display (Fig. 7.1C), we observed that people could report a maximum of four objects, which is the classic capacity limit of visual working memory (all Chapters). Moreover, working memory performance was constant over time even when the maintenance period was increased to four seconds (Chapter 2; Sligte et al., 2008). One of the more surprising findings was the observation that representations in working memory had fairly limited visual detail (Chapter 3) compared to iconic memory and fragile VSTM representations.

While iconic memory and fragile VSTM depend on neural processes in striate and extrastriate cortex, visual working memory depends on activity and brain anatomy (Chapter 6) in a widespread network of higher-level brain regions. Two key structures in this network are especially noteworthy: the superior parietal lobe (SPL) and the dorsolateral prefrontal cortex (DLPFC). The SPL seems to keep track of a maximum of three spatial locations at the same time (Todd & Marois, 2004). As can be seen in Figure 7.2, working memory capacity (K; in black) and activity in the SPL (VSTM; in red) increases with working memory load, and when working memory capacity reaches plateau so does activity in the SPL. The DLPFC, on
the other hand, seems to store a single item in working memory. In one of our studies (Chapter 4), we disrupted activity in the DLPFC with the use of transcranial magnetic stimulation to dissociate fragile VSTM from visual working memory. We observed people with high DLPFC activity stored one additional object in working memory compared to people with low DLPFC activity. Magnetic stimulation of the DLPFC destroyed this one additional representation in people with high DLPFC activity, while this manipulation has no effect in people with low DLPFC activity.

In sum, visual working memory seems to depend on a spatial system in posterior parts of the brain that indexes a maximum of three spatial locations and a central system in anterior parts of the brain that indexes a single item. It might be that the item that is indexed by both systems at the same time is the only detailed representation in working memory. The remaining representations that are indexed by the posterior network are like a file drawer system that can be used to bring other working memory information vividly to mind. The role of these networks is most likely the deployment of central and spatial attention to specific items.

![Figure 7.2](image)

**Figure 7.2** Activity in the inferior part of the intraparietal sulcus (red line) mirrors the capacity of visual working memory (black line) across set size. K is a behavioral estimate of working memory capacity, IM is activity evoked by the iconic memory condition, VSTM is activity evoked by the working memory condition.

This Figure was adopted from Todd and Marois (2004) with permission from Nature.

**A dissociation of sensory memory into two subsequent stages**

The distinction of visual short-term memory into three stages is not a completely new idea. In the early eighties, Coltheart (1980) already noted that it is unlikely that iconic memory is a unitary phenomenon (also see General Introduction, p.10-11). Instead, iconic memory seems to consist of a brief and visible persistent store that depends on stimulus luminance and
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stimulus duration and a subsequent informational persistent, non-visible store that is independent of these stimulus characteristics. Visible persistence would be a pre-categorical (or feature-based) form of short-term memory that depends on briefly persisting activity in the retina, the lateral geniculate nucleus (LGN) and primary visual cortex, while informational persistence would be a post-categorical (or object-based) form of short-term memory that depends on activity in object-based cortex, so beyond visual areas V1, V2, and V3 (see Konen & Kastner, 2008). Other scholars have proposed highly similar models in which informational persistence is denoted as “the visual analog”. These theories are in perfect harmony with the results reported in this dissertation, where iconic memory would qualify as visible persistence and fragile VSTM as informational persistence.

Depth of reverberating activity determines VSTM stage

Maintenance of information in short-term memory is usually conceptualized as a neural loop between brain areas to keep the traces of recent sensory input active after the stimuli have disappeared. Depending on what and how much brain regions are involved in these short-term memory loops, one may then predict that short-term memory can display different characteristics. If, for example, short-term memory loops are confined to visual areas V1 up to V3, short-term memory will have the typical characteristics of iconic memory; it represents unbound features and the lifetime of the memory trace depends on physical stimulus characteristics such as light intensity. This is quite logical considering that areas V1 up to V3 are involved in feature processing and not in object processing, as evidenced by a lack of neural adaptation when objects are repeatedly shown (Konen & Kastner, 2008). Loops that in addition to early visual areas- include object-specific visual areas will express object-like qualities and depending on the specific areas that are involved, short-term memory will have face-like, place-like or rectangle-like properties. Moreover, some object-specific areas have (on average) large receptive fields whereas other areas have smaller ones. Therefore, the representational capacity should be low for some stimulus categories and high for others, which is the case for fragile VSTM (Sligte, et al., 2008). Finally, when frontal and parietal regions are included in the loop, memory traces will be available for direct report and are limited by the maximum capacity of attention, which is four according to multiple object tracking studies (Cavanagh & Alvarez, 2005).

Importantly, this neural way of thinking does not strictly pose that there are three stages in VSTM. Rather, the depth of the neural loop from primary visual cortex up to parietal and frontal areas determines the capacity and the characteristics of the memory trace (for a schematic overview, see Fig. 7.3). Moreover, when we describe short-term memory traces in
this neural way, we can formulate testable predictions about “iconic memory” (brief, high-capacity, retinotopic, feature buffer), “fragile VSTM” (seconds-lasting, high-capacity, spatiotopic, object buffer), and “visual working memory” (sustained, low-capacity, view-point invariant, attentive buffer). Future work should address whether these neural predictions about VSTM hold up to the test.

Figure 7.3 Maintenance of information in visual short-term memory (VSTM) is accomplished by neural loops between brain areas. The characteristics of a specific VSTM representation depend on what brain areas are included in the neural loop; when the loop is confined to primary visual cortex, the representation is feature-based or an “iconic memory” representation; when the loop is confined to object-specific areas in extrastriate visual and temporal cortex, the representation is object-based or a “fragile visual short-term memory” representation; finally, when the loop includes areas involved with top-down attention (and many other functions), the representation is attention-based or a “visual working memory” representation. As the loops go deeper into the brain, the capacity for concurrent loops or multiple VSTM representations becomes smaller.

The relation between consciousness and visual short-term memory
“What is the biological basis of consciousness?” According to Science magazine (G. Miller, 2005), this is the second-most important scientific question that remains to be answered. Only, the question “What is the universe made of?” is deemed to be more important. This is quite funny given the fact that I once started studying Physics with the intention to unravel
the mysteries of the universe. Looking back on years of study in the field of Cognitive Neuroscience, I realize now time has brought me much closer to the other universal mystery.

Before I sketch the relation between consciousness and visual short-term memory, I will elaborate a little bit on the hard problem of consciousness; that is, the lack of a good definition. Just try to come up with a good definition yourself. Is your consciousness the stuff that thoughts are made of or does it include your experiences when you look around you with a blank mind? Is consciousness that what makes you different from other people or is it quite a common psychological process? I bet your definition of consciousness and what to include and exclude is different from my opinion and different from the opinion of the rest of the world.

To avoid this “paralyzing” lack of a unified definition, cognitive science relies on objective criteria to decide what is “conscious” and what is not. When people are able to report their experience(s) in response to a question or an instruction, this is generally taken as evidence for conscious processing. The method to collect responses may vary extensively; button presses and verbal responses ("overt responses") are traditional measures, yet recent work of Laureys and co-workers shows that even brain responses ("covert responses") might be used to probe for consciousness. Simply by asking vegetative patients to respond to questions by thinking of sports (activating motor cortex; “yes”) or by thinking of wandering around their houses (activating hippocampus; “no”), four out of 52 patients could accurately answer questions without being able to move or to respond in any overt way (Monti, et al., 2010). We must therefore conclude that these patients are conscious entities and we would not be able to deduce this from any overt behavior. Thus, brain ("covert") responses should in some cases be acknowledged as indices of consciousness.

Still, there might be situations where you were conscious for a brief moment, but you forgot your experiences before you were able to report them. To illustrate this, I will ask you to flip over to page 116 and to look at the printed picture for about ten seconds (CONTINUE HERE). Now, what did you see? Probably lemons and oranges, quite a few actually. But did you see sandwiches, bottles of wine, and bottles of beer? And what color were the pants of the vendor? And how many jugs of juice were standing on the bar?

It is very clear that when you were looking at the picture, you perceived a richly detailed and complete image. Nonetheless, you will have to acknowledge that you did not remember the entire picture with all its details after you flipped back the page. This distinction between your rich, immediate perception and the little you remember of it afterwards provides a scope onto two different kinds of awareness; perceptual awareness with high capacity and the lifetime of about a single fixation, and a more abstract form of awareness
with limited capacity and a lifetime that is related to your concentration span (see Block, 2007). We can measure these two different kinds of awareness with visual short-term memory paradigms as people store a relatively complete image of the outside world in iconic memory (Averbach & Coriell, 1961; Sperling, 1960) and fragile VSTM (Sligte, et al., 2008, 2009), and a very sparse representation in visual working memory (Luck & Vogel, 1997; Vogel, et al., 2001). Importantly, when people are asked to report their percepts from iconic memory, fragile VSTM, or visual working memory, they are able to do so. This implies that all three short-term memory stores are instances of conscious processing or at least can be equated to the availability for conscious access.

Thus, in order to increase our knowledge about the biological basis of consciousness, it is sensible to study the characteristics and neural dynamics of visual short-term memory. We might even believe that visual working memory is what remains of a directly accessible form of consciousness, while iconic memory and fragile VSTM are what remains of visual awareness without immediate cognitive access. Whether this actually is the case remains an open question.
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Figure 7.4 Quite some lemons and oranges, don’t you think so...