A new definition of visual short-term memory
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1. General Introduction

“Visual awareness is a favorable form of consciousness to study neurobiologically. We propose that it takes two forms: a very fast form, linked to iconic memory, that may be difficult to study; and a somewhat slower one involving visual attention and short-term memory.” From: Crick and Koch, 1990.

And so the quest to unravel the neurobiological basis of consciousness begins, in an era that will be dominated by techniques making it possible to look into and to manipulate the workings of the living human brain.

Take a look around you and consider how rich your percept of the visual world actually is. Then close your eyes and try to bring back a mental image of what you have just seen. Probably, you will probably realize that you remember little of what you have just seen, with the exception of a few visual “hotspots” or objects. This distinction between the richness of our immediate perception and the impoverished image we keep in memory is a compelling phenomenon and it might even provide us with a scope on how consciousness works. Exactly because of this reason, I have explored visual short-term memory processes over the past four years and the results of my research are reported in this dissertation.

Iconic memory: a derivative of our rich, visual perception

After the fall of behaviorism as the dominant line of thinking in psychology, a new era started in which we try to look into the “black box” that contains our working minds to reveal the laws of human cognition. When considering visual short-term memory (VSTM), this endeavor started with the ingenious work of George Sperling (1960) who laid the foundations of the standard model of visual short-term memory made up of 1) iconic memory that is much like a rapidly fleeting memory of our rich visual perception, and 2) visual working memory that reflects the impoverished contents of our mind’s eye.

In the following section, I will provide an in-depth view on early iconic memory research. I will emphasize the controversies that have been revealed with several different iconic memory paradigms culminating in a discussion on whether iconic memory is a unitary phenomenon or a two-partite system composed of visible persistence and informational persistence. Finally, I will talk about the neural basis of iconic memory.
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Sperling’s partial-report paradigm

The golden standard for studying iconic memory was developed by George Sperling (Sperling, 1960). In the basic design of his experiments, human observers were briefly (5-500 ms) presented with displays composed of three rows containing four letters each and they were asked to memorize all the presented items to their best ability (see Fig. 1.1A). Some time after offset of the display, the observers were asked to report as many letters as they could and people reliably report a maximum of about four letters in this “whole-report” condition, reflecting the contents and capacity limits of visual working memory.

![Figure 1.1 A. Example of Sperling’s iconic memory design. B. “Partial report” performance (iconic memory) is higher than “whole-report” performance (visual working memory) when the cue is delivered less than a second after stimulus offset. This Figure is a modified version of Figure 7 in Sperling (1960).](image)

However, when people were presented with a sound (high, medium, or low pitch indicating which row to report) immediately following the disappearance of the display, they could report almost all items of the cued row. When we follow the logic that the display containing all objects was no longer in sight, while people could still report almost all information from any specific row, we must conclude that all information had been represented in short-term memory at least for a brief period of time. To calculate the exact amount of represented information that drives performance in the “partial-report” condition, performance on a single (reported) row is multiplied by the number of rows that were presented (see Fig. 1.1B).

Initial partial-report studies suggested that the capacity of iconic memory was about 9.1 (Sperling, 1960) or 10.4 letters (Averbach & Coriell, 1961) when the cue was presented immediately after stimulus offset. These estimates most likely underestimate the capacity of iconic memory as it takes time to interpret and use the partial-report cue to retrieve
information from memory and by the time that information is retrieved some of the information in iconic memory might already have decayed. Indeed, when the partial-report cue is presented just before onset of the memory array, people are able to report up to 17 out of 18 letters (Averbach & Sperling, 1961), which implies that iconic memory capacity is virtually unlimited.

The lifetime of iconic memory can be estimated by delaying the partial-report cue with respect to the offset of the memory array, until there is no evidence anymore of superior performance on the “partial-report” condition compared to the “whole-report” condition. In general, performance on the partial-report condition declines exponentially with increases in cue delay. When using cue delays of 500 ms, there is still some evidence for superior performance on the partial report condition, but not anymore at cue delays of 1,000 ms (Averbach & Coriell, 1961; Sperling, 1960). Based on these results, the duration of iconic memory has been estimated to last for a maximum of half a second, although the exact duration does depend on the luminance of the background (Averbach & Sperling, 1961).

Moreover, iconic memory is easily masked by new visual stimulation. This is best illustrated by an experiment of Averbach and Corriell (1961), where a partial-report circle was presented around one of locations that was occupied by a letter. When the circle was presented before or during array onset, people were very good at reporting the probed letter as they just saw a circled letter. However, when the circle was presented after offset of the memory array, performance was far worse compared to ordinary partial-report cues. The circle thus seemed to mask the previously shown letter. In addition, it has been reported that complete masking of iconic memory occurs when the memory array is followed by a noise field composed of jumbled lines (Sperling, 1963).

Finally, the representational format of iconic memory seems to be a purely visual one; when partial-report cues ask people to report the location (Averbach & Coriell, 1961; Sperling, 1960), color (Clark, 1969), brightness (Von Wright, 1968), or shape (Turvey & Kravetz, 1970) of an item, a partial-report benefit over whole-report conditions is observed. However, partial-report cues that require people to report letters from an array of letters and digits (Sperling, 1960; Von Wright, 1968) or report of letters ending in the sound “ee” (Coltheart, Lea, & Thompson, 1974) do not yield a partial-report benefit. This implies that iconic memory has no semantic or phonological characteristics.

Visible persistence
Based on the characteristics described above, the modal view on iconic memory emerged (Coltheart, et al., 1974; A.O. Dick, 1974; Von Wright, 1972) that describes iconic memory as
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A brief, pre-categorical and high-capacity form of visual memory. However, this view did not last for a long period of time. Definitional problems surfaced when techniques were developed to measure the visible persistence of a stimulus beyond its duration (see (Coltheart, 1980; Long, 1980); for a complete review). An example of a visible persistence experiment it shown in Figure 1.2.

**Figure 1.2** Example of a visible persistence experiment. In the experiment, subjects first have to adjust the timing of a visual stimulus, so that it matches the onset of an auditory signal (STEP 1). Then, subjects have to adjust the timing of a second tone, so that it matches the offset of the visual stimulus (STEP 2). Now, the timing between the two tones indexes the perceived duration of the visual stimulus. By subtracting the actual visual stimulus duration from the perceived stimulus duration, one can then calculate the visible persistence of a stimulus beyond its actual duration.

In general, all visible persistence studies revealed that a stimulus evoked shorter visible persistence when the stimulus was presented longer onscreen (Bowen, Pola, & Matin, 1974; Briggs & Kinsbourne, 1972; Di Lollo, 1977; Efron, 1970; Haber & Standing, 1970) or with higher intensity/luminance (Allport, 1970; Bartlett, Sticht, & Pease, 1968; Bowen, et al., 1974; Dixon & Hammond, 1972; Efron & Lee, 1971; Haber & Standing, 1969; Pease & Sticht, 1965). These so-called inverse duration and inverse intensity effects can only be explained by retinal adaptation mechanisms; as the stimulus is presented for longer periods of time or with more intensity, the rods in the eye will fatigue more rapidly and will show a briefer after-effect after the stimulus has gone. If visible persistence equals iconic memory, one should conclude that iconic memory is related to a retinal mechanism. However, duration and intensity of the stimulus did not have any significant effects on the lifetime of iconic memory when measured with partial-report methods. As it was initially believed that partial-report and visible persistence paradigms measured the same construct (iconic memory), empirical
results were at odds with theory and new models on iconic memory were developed to explain these mixed findings.

**Two-stage models on iconic memory**
One of the earliest, “new” models of iconic memory was proposed by Coltheart (Coltheart, 1980), who argued that iconic memory should be dissociated into 1) visible persistence, and 2) informational persistence. He described visible persistence as a precategorical phenomenon caused by neural persistence in the retina and it makes us see an image or an object for a brief period of time after it has physically disappeared. Informational persistence, on the other hand, is persistence at a much higher level in the neural architecture and it provides us with categorical information of (almost) all objects in our visual field.

It seems that two-partite models of iconic memory (Coltheart, 1980; Di Lollo & Dixon, 1988; Dixon & Di Lollo, 1991) are perfectly able to explain why inverse intensity/duration effects were present in visible persistence paradigms, while they were absent in partial-report paradigms. However, most scholars still believe that iconic memory is a unitary phenomenon that is precategorical in nature. In fact, the two-partite model just described has never made it into common psychology textbooks and research on iconic memory came to a stop for a considerable amount of time after the formulation of these theories.

**The neural substrate of iconic memory**
Little is known about the neural substrate underlying iconic memory, but there are some starting points to explain the neural mechanisms of iconic memory. To begin with, electrophysiological recordings of rods and cones show that responses of photoreceptors persist beyond stimulus duration (Whitten & Brown, 1973a, 1973b, 1973c). However, iconic memory cannot be explained purely as a product of photoreceptor persistence. For instance, when rod receptors are unavailable to support iconic memory, in case of color stimuli (Banks & Barber, 1977), very small stimuli (Adelson & Jonides, 1980), or under high-luminance (Adelson & Jonides, 1980), the capacity and lifetime of iconic memory does not suffer. Cone responses persist for no more than 50 to 80 ms (Baron, Boynton, & Hammon, 1979), which is far too short to support the typical lifetime of iconic memory.

A more likely candidate to support iconic memory would be primary visual cortex as cells in primary visual cortex continue to respond after stimulus offset (Duyssens, Orban, Cremieux, & Maes, 1985), and the duration of the response is inversely related to stimulus duration, just like inverse duration effects in visible persistence studies. Nevertheless, this does not explain how informational persistence in iconic memory is achieved. There is
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actually only one study that looked into this (Keysers, Xiao, Földiák, & Perrett, 2005). In that study, partial report performance of human subjects was related to the response patterns of neurons in macaque monkeys viewing the same stimuli as the human subjects had observed (which is a very indirect way of finding a ‘neural correlate’). Activity patterns in the anterior part of the superior temporal sulcus (aSTS) seemed to mirror the accuracy patterns of human observers. Importantly, aSTS neurons do seem to share many characteristics with the properties of informational persistence as 1) responses of aSTS neurons persist for several hundreds of milliseconds, 2) independently of stimulus duration, and 3) new stimuli terminate aSTS responses (Keysers, Xiao, Foldiak, & Perrett, 2001; Kovacs, Vogels, & Orban, 1995; Rolls & Tovee, 1994).

To summarize, visible persistence seems to be related to persistence in retinal photoreceptors and in primary visual cortex. Informational persistence on the other hand depends on lingering activity in areas higher up in the visual hierarchy. Nevertheless, the exact neural mechanisms underlying iconic memory remain to be elucidated.

Visual working memory: the impoverished contents of the mind’s eye

Research on iconic memory thus shows that people continually build up a brief internal picture of the outside world. This high-capacity picture is overwritten each time we make an eye movement or when a new image is displayed on a computer screen to make way for a new high-capacity internal picture. Still, when we lay our eyes on a pretty person walking by, we are able retain his/her appearance in mind for some time with a surprising amount of detail, even in the face of the continuous arrival of new visual information. This kind of memory - that is resistant to overwriting - is usually called visual working memory.

In the following section, I will introduce the change detection paradigm that is commonly used to measure visual working memory. In addition, I will talk a little bit about the neural substrate underlying visual working memory.

The change detection paradigm

One of the striking aspects of visual working memory is its severe capacity limit and this can be illustrated beautifully with change detection experiments. In standard change detection experiments performed in the lab (see Fig. 1.3), people are shown a memory display (or sample display) containing multiple objects or a complex natural scene and they are asked to memorize the entire image to their best ability. After a brief retention delay, a test display (or probe/match display) is shown in which one of the objects or parts of the scene have changed with respect to the memory display on 50 percent of the trials and subjects have to
indicate whether there was a change between displays or not. In general, people perform badly on change detection tasks, even when changes are as large as a jet engine or a building disappearing.

The apparent blindness to changes can be well explained; usually, changes in the environment are accompanied by a motion signal that automatically captures attention (Rensink, 2002; Simons & Rensink, 2005). When capture of attention is prevented by masking the change (in this case by interposing a blank interval), people have to rely on top-down information that is represented in visual working memory. As the capacity of visual working memory is very limited, change blindness is the rule rather than the exception. Note that iconic memory is of no help here as the new stimulation after the blank interval overwrites iconic traces and renders them ineffective.

Figure 1.3 Two examples of change detection tasks. People are asked to memorize a display and after a blank interval of at least 80 ms a test display is shown in which there is a change in 50 percent of the trials. Subjects have to indicate on each trial whether there is a change or not between successive displays. In the above examples, there is a change in both cases.

So far, it has been shown that visual working memory has a maximum capacity of four integrated objects (Luck & Vogel, 1997; Vogel, Woodman, & Luck, 2001), although capacity limits seems to be stricter for more complex stimulus material (Alvarez & Cavanagh, 2004; Eng, Chen, & Jiang, 2005; Olsson & Poom, 2005). For instance, when people have to remember multiple faces or Chinese characters, they can only remember one or two objects.
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at a time. Also, when the objects to remember are simple, but the change between memory and test display is very small, people perform badly on change detection tasks (Bays & Husain, 2008).

The neural substrate underlying visual working memory

Initial studies in macaque monkeys showed that the dorsolateral prefrontal cortex (DLPFC) was crucial for working memory maintenance as lesions of this region (within and around the principal sulcus; BA 46) greatly impaired working memory performance (Goldman and Rosvold, 1970; Bauer and Fuster, 1976; Funahashi et al., 1993). In addition, single-cell recordings from the DLPFC revealed sustained activity during the delay of visual working memory tasks (Funahashi, Bruce, & Goldman-Rakic, 1989, 1990, 1991; Fuster & Alexander, 1971; E. K. Miller, Erickson, & Desimone, 1996).

Subsequent functional MRI studies revealed that the DLPFC was also active in man during visual working memory maintenance (Courtney, Ungerleider, Keil, & Haxby, 1997; Curtis, 2006; Curtis & D'Esposito, 2003; Pessoa, Gutierrez, Bandettini, & Ungerleider, 2002). Additionally, it was found that visual working memory maintenance was related to activity in the anterior cingulate cortex (ACC), the frontal eye fields (FEF), the posterior part of the middle frontal gyrus (pMFG), the intraparietal sulcus (IPS), the superior parietal lobe (SPL), and many high-level visual areas in visual and temporal cortex (see Fig. 1.4 for a typical activation pattern during visual working memory maintenance; adopted from Pessoa et al., 2002 with permission).

Even primary visual cortex seems to be important for visual working memory maintenance. In a study of Supér, Spekreijse and Lamme (2001), monkeys performed delayed eye movements to briefly presented figures. By either presenting the figure inside the receptive field (RF) that was measured with single-cell recordings or outside the RF, it was possible to isolate delay activity related to the representation of the figure in working memory. It was evident that there was more activity when the figure was inside the measured RF compared to when it was outside the measured RF over a delay of maximally two
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seconds and this additional activity was task-relevant; when a new, but irrelevant display was shown the additional working memory related activity was still present after the display, but not when the monkey had to react to the intervening display. In addition, on a proportion of trials the monkeys did not make an eye movement after the delay and on these missed trials the additional activity related to the figure representation was present for a short period of time (probably reflecting iconic memory), but collapsed before the delay was over. Recently, the group of Frank Tong also found working memory-related activity in primary and secondary visual cortex in human subjects (Harrison & Tong, 2009).

Altogether, visual working memory maintenance seems to depend on the orchestrated cooperation of a widespread network of brain regions. Whether all these areas are involved with stimulus maintenance or whether particular brain areas subserve other functions are necessary for working memory maintenance, such as top-down attention and control, remains, for now, an open question.

A third form of visual short-term memory?

To complicate matters, recent work from our lab has suggested the existence of a third form of visual short-term memory (VSTM) that outlasts the lifetime of iconic memory and at the same time has twice the capacity of visual working memory. This new form of VSTM can be measured by combining the partial-report, iconic memory paradigm with the change detection, working memory paradigm. In the general set-up of the experimental paradigm, a partial-report cue is shown during the delay of a change detection task and the partial-report cue retrospectively singles out the item to change. Several studies have so far shown that partial-report cues dramatically boost change detection performance (Griffin & Nobre, 2003; Landman, Spekreijse, & Lamme, 2003; R. Landman, Spekreijse, & Lamme, 2004) compared to when the cue is presented after the change. Then, capacity is limited to 4 objects, which is the well-known limit of visual working memory (Luck & Vogel, 1997; Vogel, et al., 2001). Moreover, increases in change detection performance caused by a partial-report cue are not due to speed-accuracy trade-offs (Griffin & Nobre, 2003; Lepsien, Griffin, Devlin, & Nobre, 2005), response biases (Griffin & Nobre, 2003), eye movements (Griffin & Nobre, 2003; Matsukura, Luck, & Vecera, 2007), or articulation (Makovski & Jiang, 2007; Makovski, Sussman, & Jiang, 2008).

Importantly, partial-report cues boost change detection performance even when they are presented four seconds after stimulus disappearance (Lepsien & Nobre, 2007), which is far beyond the lifetime of iconic memory. In addition, elementary feature binding seems to be present in this form of VSTM (Landman, et al., 2003; R. Landman, et al., 2004), an
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observation that has never been made in relation to iconic memory. Thus, this seconds-lasting and bound form of VSTM seems to be something entirely different from either iconic memory or visual working memory, and even the idea of Coltheart that iconic memory consists of visible and informational persistence does not fit with a seconds-lasting, high-capacity and bound form of VSTM.

Thesis outline
The present dissertation aims to unravel the behavioral characteristics and the neural substrate of this new and intermediate VSTM store and how it differs from iconic memory and visual working memory both on the behavioral and the neural level.

In Chapter 2, I will describe a series of experiments that provides evidence that visual short-term memory (VSTM) consists of three stages; 1) an extremely high-capacity, but brief form of visual memory that depends on an after-image in the retina (“iconic memory”), 2) a relatively high-capacity and seconds-lasting form of visual memory that is independent of retinal mechanisms (“weak or fragile VSTM”), and 3) a sustained form of visual memory with limited capacity (“visual working memory”). In Chapter 3, I will present evidence that representations in iconic memory and fragile VSTM are visually detailed or high-resolution representations, while visual working memory representations are mostly abstract representations. In Chapter 4, I will show that that the right dorsolateral prefrontal cortex (DLPFC) is crucial for visual working memory maintenance, but not for maintenance of representations in fragile VSTM, thereby dissociating these two VSTM stages from each other. In Chapter 5, I will show that activity in visual area V4 predicts whether an item is represented in fragile VSTM or in visual working memory. In Chapter 6, I will show that brain anatomy constrains the capacity of iconic memory, fragile VSTM and visual working memory, albeit at different levels in the visual hierarchy.

Together, the findings reported in this dissertation argue for a new and tri-partite model of VSTM that dissociates 1) iconic memory, a low-level and brief form of VSTM that depends on prolonged retinal firing beyond stimulus duration that in turn drives neural processes in primary visual cortex, 2) fragile VSTM, a medium-level and relatively sustained form of VSTM that depends on activity in object-selective visual areas, and 3) visual working memory, a high-level and sustained form of VSTM that depends on activity in parietal and prefrontal cortex in addition to activity in visual parts of the brain.
Publications

All chapters in this thesis are published or submitted for publication in international peer-reviewed journals.


