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Magnetic stimulation of the dorsolateral prefrontal cortex dissociates fragile visual short-term memory from visual working memory

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ABSTRACT

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). While VSTM is usually broken down into iconic memory (brief and high-capacity store) and visual working memory (sustained, yet limited-capacity store), recent studies have suggested the existence of an additional and intermediate form of VSTM that depends on activity in extrastriate cortex. In previous work, we have shown that this fragile form of VSTM can be dissociated from iconic memory. In the present study, we provide evidence that fragile VSTM is different from visual working memory as magnetic stimulation of the right dorsolateral prefrontal cortex (DLPFC) disrupts visual working memory, while leaving fragile VSTM intact. In addition, we observed that people with high DLPFC activity had superior working memory capacity compared to people with low DLPFC activity, and only people with high DLPFC activity really showed a reduction in working memory capacity in response to magnetic stimulation. Altogether, this study shows that VSTM consists of three stages that have clearly different characteristics and rely on different neural structures. On the methodological side, we show that it is possible to predict individual susceptibility to magnetic stimulation based on functional MRI activity.

1. Introduction

Our brain essentially acts as a filter that reduces the amount of available information at each subsequent step in the neural hierarchy. This mechanism is especially evident when looking at different stages in visual short-term memory (VSTM). Initially, people build up a high-capacity representation in iconic memory (Sperling, 1960) that is related to persistence in retinal photoreceptors (Sligte, Scholte, & Lamme, 2008) and primary visual cortex (Duysens, Orban, Cremieux, & Maes, 1985) beyond stimulus duration. Iconic memory is usually measured by presenting a memory array containing multiple rows of letters. Then, after offset of the memory array, a partial-report cue is shown that singles out the row to report. When this partial-report cue immediately follows memory array offset, people can report almost all letters from any specific row, suggesting that all or at least a large amount of items are stored (Averbach & Coriell, 1961; Sperling, 1960). Iconic memory traces are short-lived as they can only be measured over the first half second after memory array offset and they are extremely volatile as well (Averbach & Coriell, 1961; Sperling, 1963); each time a new image hits our retina, iconic memory is erased 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 to retain his/her appearance in mind for some time, 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. 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 Figs. 1, bottom, and 2, top for examples), people are shown a memory display containing multiple objects or a complex scene and they are asked to memorize the entire image. After a brief retention interval, a test display (or probe/match display) is shown in which one of the objects has changed with respect to the memory display on 50% 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 (Rensink, O'Regan, & Clark, 1997).

This apparent blindness to changes can be well explained; usually, changes in the environment are accompanied by motion signals that automatically capture attention (Rensink, 2002; Simons & Rensink, 2005). However, 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 change blindness is the rule rather than the exception, top-down resources are apparently very sparse; it has been estimated that visual working memory

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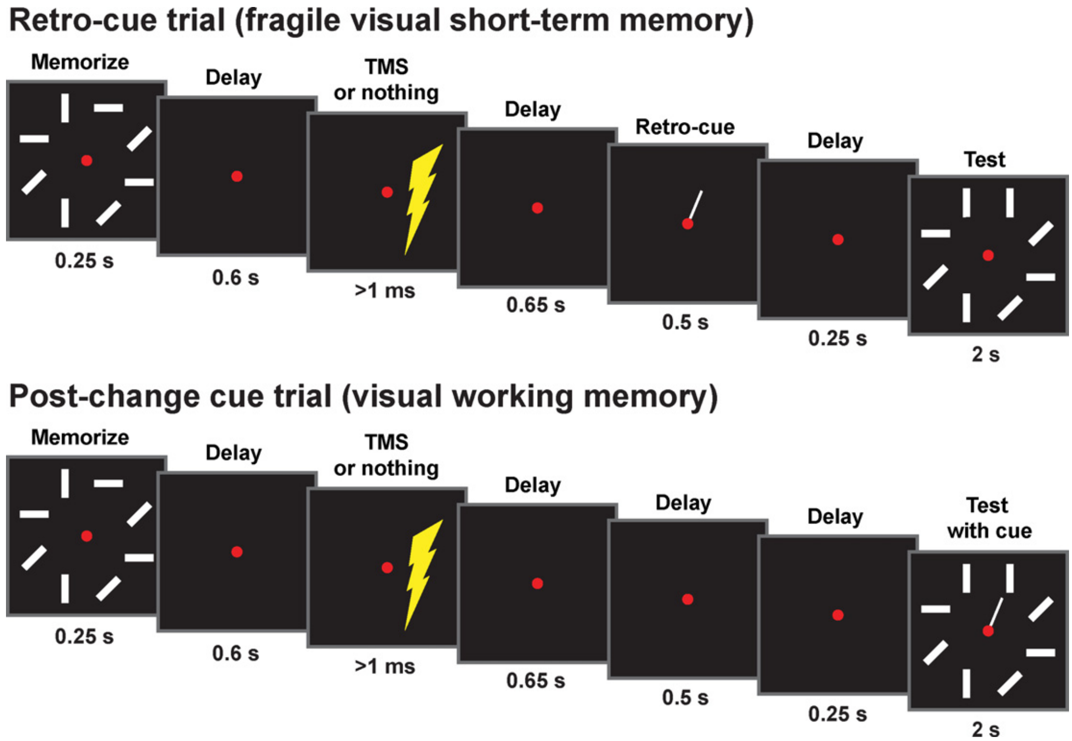

Fig. 1. Subjects performed a visual short-term memory task, in which they had to detect changes that occurred between a memory and a test display. In addition, attention-directing cues were presented during the retention interval (retro-cue trial) or thereafter during the test display (post-change cue trial). Typically, people can report up to 15 items (out of 32) on retro-cue trials, but no more than 4 items on post-change cue trials; this reflects the capacity of fragile visual short-term memory representations and the capacity of visual working memory, respectively. On 50% of the trials, single-pulse transcranial magnetic stimulation (TMS) was applied to the right dorsolateral prefrontal cortex (DLPFC), 600 ms after offset of the memory display.

contains a maximum of four integrated objects (Luck & Vogel, 1997; Vogel, Woodman, & Luck, 2001), although capacity limits seem to be stricter for more complex stimulus material (Alvarez & Cavanagh, 2004; Eng, Chen, & Jiang, 2005; Olsson & Poom, 2005). Note that iconic memory is of no help in change detection tasks as new stimulation after the blank retention interval overwrites iconic traces and renders them ineffective.

While the modal view of VSTM consists of iconic memory and visual working memory, recent work from our lab has suggested the existence of a new form of VSTM that operates in between iconic memory and visual working memory. We first came across this intermediate form of VSTM when we combined a partial-report, iconic memory paradigm with a change-detection, working memory paradigm (Landman, Spekreijse, & Lamme, 2003). In the design of this combined task (see Fig. 1, top), a spatial cue is shown during the delay of a change detection task and this cue retrospectively singles out the item to change. This cue is often referred to as a retro-cue. It requires subjects to orient their attention to a specific location in VSTM and to retrieve the information that was presented at that location before, in the prior memory display.

Several studies have so far shown that retro-cues dramatically boost change detection performance (Griffin & Nobre, 2003; Landman et al., 2003; Landman, Spekreijse, & Lamme, 2004; Sligte et al., 2008) compared to when the cue is presented after the change (so-called post-change cue). Then, capacity is limited to four objects, which is the well-known limit of visual working memory (Luck & Vogel, 1997; Vogel et al., 2001). Recently, we found that when a retro-cue was presented one second after offset of the memory display, people could report up to 15 out of 32 objects (Sligte et al., 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 one 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 retro-cue was presented 4 s after stimulus offset, people still had access to more information than could fit in their visual working memory (Lepsien & Nobre, 2007; Sligte et al., 2008; Sligte, Scholte, & Lamme, 2009). Importantly, increases in change detection performance caused by a retro-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).

To rule out that this high-capacity and relatively long-lasting memory store (from now on termed *fragile VSTM*) was a reflection of either iconic memory or visual working memory, we performed a series of behavioral and neuroimaging experiments (Sligte et al., 2008, 2009; Sligte, Vandenbroucke, Scholte, & Lamme, 2010). From our behavioral experiments, it was evident that fragile VSTM was not a form of iconic memory as (1) differences in stimulus contrast had no influence on fragile VSTM capacity, but a profound effect on iconic memory capacity (Sligte et al., 2008), (2) the presence of light flashes (Sligte et al., 2008) or homogeneous textures (Landman et al., 2003, 2004) during retention erased iconic memory, but did not affect fragile VSTM capacity, and (3) features were bound into coherent objects in fragile VSTM, a characteristic that has never been observed in relation to iconic memory (Landman et al., 2003, 2004). On a neural level, we observed that fragile VSTM produced an increase in V4 activity at the retinotopic location corresponding to the item held in fragile VSTM (Sligte et al., 2009). In contrast, the neural site of iconic memory seems to be at a lower level in the neural hierarchy (Duysens et al., 1985; Sligte et al., 2008). Thus, based on findings from behavioral and neuroimaging studies we can dissociate fragile VSTM from iconic memory.