Cyprus University of Technology

Faculty of Health Sciences

Doctoral Dissertation

EXPLORING THE SENSORY RECRUITMENT FRAMEWORK: THE ROLE OF THE SENSORY VISUAL CORTEX IN VISUAL SHORT-TERM MEMORY

PHIVOS PHYLACTOU

Limassol, May 2023

CYPRUS UNIVERSITY OF TECHNOLOGY

FACULTY OF HEALTH SCIENCES

DEPARTMENT OF REHABILITATON SCIENCES

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Approval Form

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Limassol, May 2023

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Acknowledgements.

One of the first ever books that I started reading was called “*Rich Dad Poor Dad*” by Kiyosaki and Lechter (2021). It was a terrible book and I hated it. In fact, I never even finished it. In any case, I’m borrowing their idea to acknowledge my “*Academic Dad*”, Dr. Nikos Konstantinou, who happened to be my supervisor during this amazing start of my academic journey. Nikos has been a mentor, a role-model, and a friend. Without his passion, effort, and contribution, I would have never been able to produce any of the work presented here. That does not mean that I will finish reading “*Rich Dad Poor Dad*”, though.

Of course, many others have also significantly contributed and helped with the production of this work, in many ways. Namely, I want to thank Dr. Artemis Traikapi, Dr. Marietta Papadatou-Pastou, Dr. Andria Shimi, and Prof. Nilli Lavie, who contributed on the science presented in my thesis.

Further, I express my appreciation to every single colleague in the Department of Rehabilitation Sciences of Cyprus University of Technology, for the fruitful discussions (whether scientific or simply social), every single individual who voluntarily offered their time to participate in my experiments, and of course my family and friends, who, despite having no idea what I am doing, have always pretended to care when I bombarded them with my academically related non-sense.

ABSTRACT

The sensory visual cortex (SVC) is involved in encoding information in visual short-term memory (VSTM). Yet, it remains unclear if the SVC is a necessary component of the brain network necessary for maintaining information in VSTM. The aim of this thesis was to shed light on the debated role of the SVC in VSTM. Thus, I focused on transcranial magnetic stimulation (TMS). TMS uses a coil to transfer electromagnetic stimulation at localized brain areas making the exploration of causal evidence plausible. Through a systematic review and meta-analysis of previous SVC TMS studies I indicated that the SVC is similarly involved in both the encoding and maintenance VSTM phase, and that the controversy was likely due to methodological issues in TMS studies. Building on these findings I conducted two TMS experiments that covered the previous methodological oversights by ensuring the monocular presentation of orientation stimuli. TMS was delivered at different times during the maintenance phase of a delayed change-detection VSTM task, on one side of the occipital hemisphere. Decreased VSTM performance in the ipsilateral occipital hemisphere to visual hemifield, and in the real TMS (compared to sham TMS) condition indicated inhibitory TMS effects, and thus, a causal involvement of the SVC during VSTM maintenance. After establishing the role of the SVC in VSTM maintenance through TMS, I turned to memory load manipulations to further investigate the relationship between short-term memory and perception. I combined short-term memory tasks with perceptual detection tasks, where I manipulated the sensory load of the memory items and measured the effect of this load manipulation on perceptual detection. A combined VSTM and visual perception task provided additional evidence in favor of the sensory recruitment framework, since visual detection was reduced due to the increased VSTM load. Evidence against any cross-modal effects between VSTM and auditory perception was found, and evidence from a combined auditory short-term memory and auditory perception task indicated that sensory recruitment was not supported for the auditory modality. Overall, my findings support the sensory recruitment framework of VSTM, which proposes that sensory visual areas have a dual function: they are involved in the precise sensory encoding of elemental visual features and the short-term maintenance of this information.

Keywords: visual short-term memory, working memory, sensory visual cortex, sensory recruitment, visual cortex

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LIST OF ABBREVIATIONS

ASTM	Auditory Short-Term Memory
BOLD	Blood-Oxygenation Level Dependent
EEG	Electroencephalography
fMRI	Functional Magnetic Resonance Imaging
IT	Inferotemporal Cortex
PFC	Prefrontal Cortex
PPC	Posterior Parietal Cortex
ROI	Region of Interest
SDT	Signal Detection Theory
SVC	Sensory Visual Cortex
TMS	Transcranial Magnetic Stimulation
VSTM	Visual Short-Term Memory
WM	Working Memory

1 General Introduction

1.1 Preface

When it comes to temporarily remembering visual information, the most vital cognitive system is Visual Short-Term Memory (VSTM). VSTM enables us to maintain in mind, for a few seconds (approximately up to 30 seconds), visual representations that are no longer present, to complete task-oriented goals (Baddeley, 1986, 2000a; Baddeley & Hitch, 1974; Luck, 2008; Repovš & Baddeley, 2006; for recent reviews see D'Esposito & Postle, 2015; Lorenc & Sreenivasan, 2021). Per se, VSTM protects visual information against interference, making representations available for cognitive processing, and thus provides the essential link between perception and higher cognitive functions, underpinning our ability for complex thought and action (Fukuda et al., 2010; Luck & Vogel, 2013). For more than half a century, cognitive scientists have attempted to understand the neural underpinnings of VSTM (e.g., Fuster & Alexander, 1971) to unravel how the brain successfully maintains visual information for short periods of time. Currently, it is well-established in the literature that frontal (Christophel, Allefed, et al., 2018; Funahashi, 2017; Levy & Goldman-Rakic, 2000; Riley & Constantinidis, 2016) and parietal (Bettencourt & Xu, 2016; Ester et al., 2015, 2016; Xu & Chun, 2006) brain areas are associated with VSTM. However, the role of the sensory visual cortex (SVC) in VSTM still remains under debate. Specifically, according to the sensory recruitment framework, neurons in the SVC that show selective activation for specific elemental visual features, such as orientation, are also ideal candidates for storing this information during VSTM (Harrison & Tong, 2009; Serences et al., 2009; Supèr et al., 2001). On the contrary, recent reviews opposed the sensory recruitment framework, arguing that VSTM storage in the SVC is impossible, because of its susceptibility to the constant processing of new incoming visual information (Xu, 2017, 2018, 2020). In this thesis I explore the controversial role of the SVC in VSTM, and present evidence in favor of the sensory recruitment framework, in an effort to shed light on this debate. I begin with this introductory chapter, where I present the current state of VSTM frameworks, starting from a historical view and leading to the most contemporary theories of VSTM. Further, I describe the current debate in cognitive science regarding the role of the SVC in VSTM, the available methods to investigate the neural corelates of VSTM, and how this thesis can provide an understanding for the contradicting role of SVC in VSTM.

1.2 Frameworks of Visual Short-Term Memory: The State-of-the-Art

1.2.1 The History of Visual Short-Term Memory Theories

Understanding the cognitive system of memory had drawn early scientific interest. The very first attempt of conceptualizing memory into a framework came in the nineteenth century from the work of William James (1890), who introduced a two-systems memory model consisting of primary and secondary memory. This theory inspired future work (Evans, 1990), which proposed different frameworks of memory, such as Broadbent's Filter Model of Attention (Broadbent, 1958) and Waugh and Norman's (1965) Primary Memory Model. However, in the mid-twentieth century, the most widely accepted framework of memory was the Modal Model of Memory, proposed by Atkinson and Shiffrin (1968). In the Modal Model of Memory (Atkinson & Shiffrin, 1968), memory consists of three information stores namely, (i) sensory memory, (ii) short-term memory, and (iii) long-term memory (Figure 1.1).

Figure 1. 1: The Modal Model of Memory (Atkinson & Shiffrin, 1968).

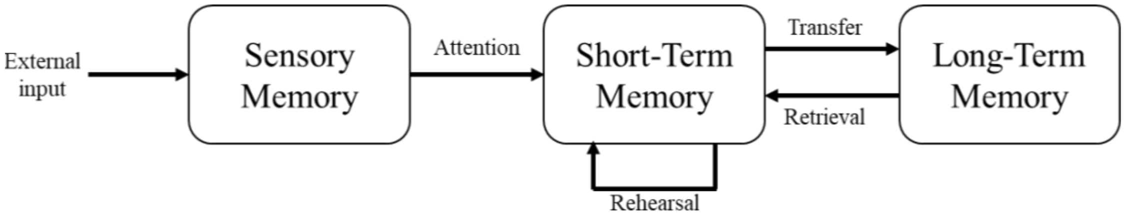

Fig.1.1. The Modal Model of Memory proposes that memory consists of three information systems. The sensory memory, which processes external input, the short-term memory, which processes attended stimuli from sensory memory and uses rehearsal to maintain them, and the long-term memory, which stores transferred information from short-term memory that can also be later retrieved.

Around the same time of the introduction of the Modal Model of Memory (Atkinson & Shiffrin, 1968), the term Working Memory (WM) appeared in the cognitive science literature (Miller et al., 1960; Pribram et al., 1960), which describes information processing of memory representations, which are no longer present in the environment

(Aben et al., 2012; Cowan, 2008; Postle, 2006)[1]. The introduction of WM, led many scientists to explore and further understand short-term memory, resulting to frameworks specific to conceptualizing WM. The most influential WM framework is the Multi-Component Model of Working Memory proposed by Baddeley and Hitch (1974). The initial Multi-Component Model of Working Memory (Baddeley & Hitch, 1974) was later revised (Baddeley, 1986, 2000a), leading to a WM framework still widely accepted today (see Chai et al., 2018). The revised Multi-component Model of Working Memory (Baddeley, 2000) described that WM consists of four components: (1) the phonological loop, which processes sound or phonological information, (2) the visuospatial sketchpad, which processes visual information, (3) the central executive, which regulates the cognitive system, and (4) the episodic buffer, which links phonological and visuospatial information across domains (Figure 1.2).

Figure 1. 2: The Multi-Component Model of Working Memory (Baddeley, 2000).

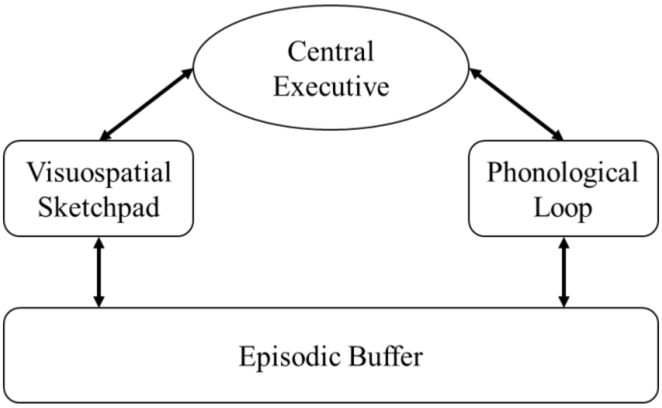

Fig.1.2. The multi-component model of Working Memory consists of the phonological loop (sound or phonological information processing), the visuospatial sketchpad (visual information processing), the central executive (cognitive system control), and the episodic buffer (phonological and visuospatial information linking)

Recently, following a large body of evidence regarding VSTM, the Multi-Component Model of Working Memory, was once more revised, with a focus on the visual domain (Baddeley et al., 2011; Hitch et al., 2020). In the latest revisit of the model (Hitch et al., 2020), the role of attentional mechanisms, such as attentional refreshing (i.e., encoding stimuli similar to previously encoded ones) and task set filters (i.e., task-related perceptual filters), are being recognised in the framework (Figure 1.3).

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[1] Here it is important to note that in the VSTM literature, the terms *visual short-term memory* and *visual working memory* are used interchangeably (Luck & Vogel, 1997). Despite some work suggesting a distinction between the two processes (e.g., Aben et al., 2012; Cowan, 2008), in this thesis, I consider VSTM and visual WM to refer to the same cognitive process.

Figure 1. 3: The revised visual domain of the Multi-Component Model of Working Memory (Hitch et al., 2020).

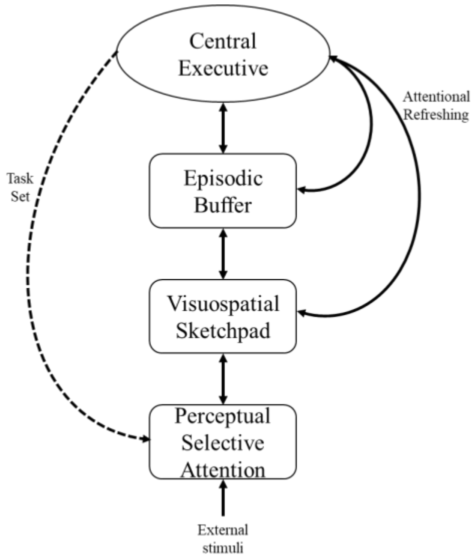


Fig.1.3. In a recent revision of the Multi-Component Model of Working Memory, the role of task-related perceptual filters (task set) and attentional mechanisms (attentional refreshing), were included in the model, as part of the visual short-term memory system.

The frameworks of WM have influenced cognitive neuroscience and the investigation of the neural mechanisms underlaying WM. As I discuss next, the Multi-Component Model of Working Memory (Baddeley, 1986, 2000a; Baddeley & Hitch, 1974), has influenced the initial attempts of understanding the neural architecture of WM.

1.2.1.1 The Multi-Component Model of Working Memory and the Brain

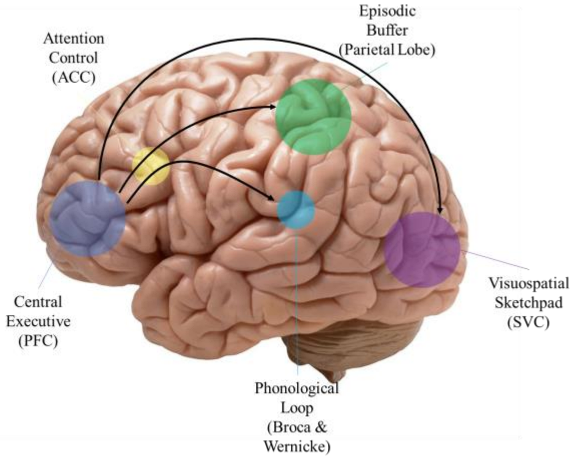
Along with the first attempt of modelling WM (Baddeley & Hitch, 1974), came the first body of evidence from electrophysiological studies in primates regarding WM. These studies indicated that when primates held representations in WM, neurons in the prefrontal cortex (PFC) were persistently firing (Fuster, 1973; Fuster & Alexander, 1971; Niki, 1974). Building on neurophysiological evidence linking the PFC with WM (Funahashi et al., 1989, 1990; Fuster, 1973; Fuster & Alexander, 1971; Fuster et al., 1982; Niki, 1974; Niki & Watanabe, 1976; Quintana et al., 1988; Watanabe, 1981), Goldman-Rakic (1987, 1995) suggested that the Central Executive component of the Multi-Component Model of Working Memory (Baddeley, 1986; Baddeley & Hitch, 1974) was a process controlled by the PFC.

At the time, VSTM, the cognitive system responsible for maintaining visual information in WM (D’Esposito & Postle, 2015; Fukuda et al., 2010; Luck, 2008; Luck & Vogel, 2013; Repovš & Baddeley, 2006), was also seen as part of the Multi-Component Model of Working Memory (Postle, 2006; see also Baddeley & Logie, 1999; Logie, 1986, 1995), following supporting neurophysiological evidence linking VSTM with the Central Executive component controlled by the PFC (e.g., Della Sala et al., 1999; Hecker & Mapperson, 1997; Mecklinger & Muller, 1996; Tresch et al., 1993; Wilson et al., 1993). After linking the Central Executive with the PFC, subsequent work investigated the relationship of specific brain areas with other components of the model, such as the involvement of the anterior cingulate cortex and the parietal cortex with attentional control and the episodic buffer, respectively (Chein et al., 2011; Kim et al.,2015; Osaka et al., 2003; Owen et al., 2005), as well as Broca's and Wernicke's areas with the phonological loop and the SVC with the visuospatial sketchpad (see Baddeley, 2000b). This neuroscientific binding of the Multi-Component Model of Working Memory with the different brain areas is shown in Figure 1.4 (see also Chai et al., 2018).

This modular view of WM, where each brain area is considered to be involved with a particular role in WM, has led to an important understanding of the neural architecture of VSTM. However, as I explain next, more contemporary frameworks of VSTM, argue that a modular view of WM, is insufficient to understand the neural underpinnings of short-term visual information maintenance.

Figure 1. 4: Linking the Multi-Component Model of Working Memory with specific brain areas.

Fig.1.4. Brain areas associated with the components of the Multi-Compenent Model of Working memory. ACC; Anterior Cingulate Cortex, PFC; Prefrontal Cortex, SVC; Sensory Visual Cortex.



1.2.2 Contemporary Theories of Visual Short-Term Memory

Following this modular view of WM, together with the technological advancements that introduced new experimental methods to cognitive neuroscience (see section *1.3.1 Studying the Sensory Visual Cortex in Visual Short-Term Memory* for an overview), numerous findings emerged for specific brain areas contributing to VSTM. Further to the currently well-established role of frontal (Christophel, Allefed, et al., 2018; Funahashi, 2017; Levy & Goldman-Rakic, 2000; Riley & Constantinidis, 2016) and parietal (Bettencourt & Xu, 2016; Ester et al., 2015, 2016; Xu & Chun, 2006) brain areas in VSTM, at the beginning of the twenty-first century, evidence for the role of the SVC in VSTM appeared in the literature (Harrison & Tong, 2009; Serences et al., 2009). However, one of the currently ongoing controversies in cognitive science (see Shevlin, 2020) relates to the role of the SVC in VSTM (described in detail in section *1.3.2 The Sensory Recruitment Hypothesis Debate*). As explained below, contemporary VSTM frameworks, recognise that part of this debate, stems from adopting a modular view of WM, where hypotheses focus on whether a brain area is essential (or not) for the short-term maintenance of visual information, based on evidence from persistent activity of neurons during VSTM.

Today, neuroscience approaches cognition under two views: the Sherringtonian view and the Hopfieldian view (Figure 1.5; Barack & Krakauer, 2021; see also Krakauer, 2022). According to the Sherringtonian view, cognition can be explained by specific neuronal connections or brain areas (e.g., Parker, 2006; Tye, 2018), similar to the modular view of WM described in the previous section. On the other hand, the Hopfieldian view suggest that cognition is explained by how representations are computed across neural spaces (e.g., Hopfield, 1982, 1984; Hopfield & Tank, 1986), which can be distributed across the brain, rather than in one specific brain area. Similarly with the Hopfieldian view of cognition, it has been argued that in order to understand the neural basis of VSTM, a modular approach is inadequate to explain the neural underpinnings of VSTM (Christophel, Allefed, et al., 2018; Christophel et al., 2017; D’Esposito & Postle, 2015; Lorenc & Sreenivasan, 2021; Postle, 2006, 2015, 2016; Teng & Postle, 2021; see also section *1.3.3 A Distributed View: The Sensory Recruitment Framework*).

Therefore, contemporary theories of WM, propose a distributed framework of VSTM, which recognises the possibility that certain brain areas can be flexibly involved depending on the circumstances and VSTM task demands (D’Esposito & Postle, 2015; Scimeca et al., 2018; Postle, 2006, 2015, 2016; Teng & Postle, 2021). The distributed VSTM framework suggests moving beyond studying the essential involvement of certain brain areas in VSTM and towards understanding how VSTM representations are handled and distributed across the brain network in order to guide behavior (Christophel et al., 2017; Lorenc & Sreenivasan, 2021; Teng & Postle, 2021).

Figure 1. 5: A simplified visualization of the Sherringtonian and Hopfieldian views.

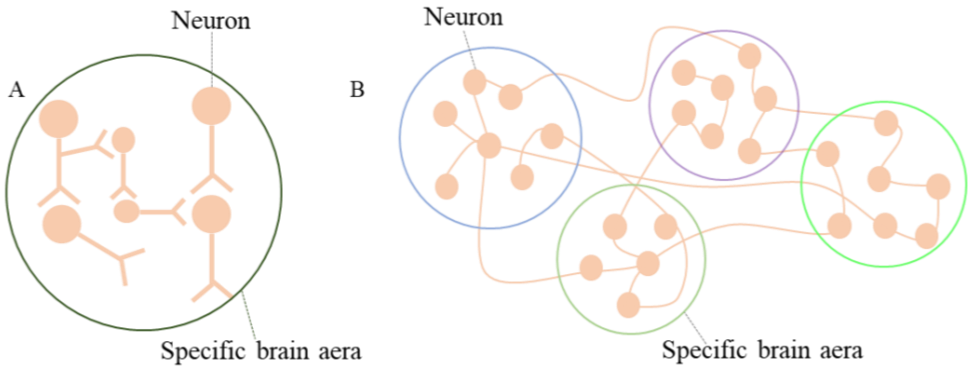


Fig.1.5. (A) The Sherringtonian view proposes that cognition can be understood by studying specific neuronal connections within certain brain areas. (B) The Hopfieldian view suggests that in order to understand cognition the focus should be turned to how representations are distributed across neural spaces.

As previously mentioned, WM research has traditionally followed a modular aproach for understanding the neural basis of VSTM (i.e., *if* a brain area is essential), which was mainly driven by the persistent firing of neuronal activity in a given brain area during remembering. Contemporary VSTM theories proposed transitioning from the modular view of *if* towards a distributed view of *how* a brain area contributes to maintaining visual information (Christophel et al., 2017; Lorenc & Sreenivasan, 2021; Teng & Postle, 2021). As described below (see *1.3.3 A Distributed View: The Sensory Recruitment Framework*) this contemporary VSTM view of *how* a brain area contributes to VSTM, acknowledged different VSTM storage mechanisms, other than the traditional persistent activity of neurons, such as synaptic weight activity-silent processes (Masse et al., 2020) as well as modulations due to context related tasks and goals (Lorenc & Sreenivasan, 2021). Therefore, under this contemporary distributed view of VSTM, it is proposed that persistent activity is not the sole neural marker that can signify the involvement of a specific brain area in VSTM (Lorenc & Sreenivasan, 2021; Masse et al., 2021; Teng & Postle, 2021). Thus, in this thesis I espouse this notion, and explore the debated role of SVC in VSTM using approaches that can account for the limitations of persistent neural activity, in order to reach a comprehensive understanding of the debate. Next, I turn to a detailed description of the previous findings encompassing the role of the SVC in VSTM, and the contradictions that led to its debated involvement in the short-term maintenance of visual information.

1.3 Sensory Recruitment: Hypothesis or Framework?

1.3.1 Studying the Sensory Visual Cortex in Visual Short-Term Memory

In order to explore VSTM scientists have been using computerised WM tasks, which closely resemble the way in which our visual short-term memory system is used in the natural environment. For example, our visual input is frequently interrupted by periods of suppressed visual processing caused by blinks and eye movements, and VSTM presumably plays an important role in comparing a memory representation of the visual input formed before the interruption with the new input that is available after the interruption. As shown in Figure 1.6, these VSTM tasks contain a memory sample, a retention interval, and a memory probe (e.g., Luck & Vogel, 1997, Vogel et al., 2001; Zhao et al., 2022) and participants are asked to either match the probe with the memory sample (VSTM delayed match-to-sample task) or detect whether there is a change (usually 50% of the trials) between the memory probe and memory sample (VSTM delayed change-detection task). The main advantage of such VSTM paradigms is that they involve only relatively simple processes, making task performance sensitive primarily to the nature of the short-term maintenance of visual information. In addition, these computerised delayed match-to-sample and change-detection tasks can be combined with various neuroscientific methodological tools to explore the role of the SVC in VSTM.

As discussed in more detail below, in 2009 two pioneering studies presented evidence that the SVC is a likely candidate to maintain elemental visual features in VSTM (Harrison & Tong, 2009; Serences et al., 2009; for more details see section *1.3.1.3 Functional Magnetic Resonance Imaging Studies*). These findings introduced the *sensory recruitment hypothesis*, according to which sensory visual areas are necessary for the successful sensory specific maintenance of basic visual features in VSTM (Harrison & Tong, 2009; Serences et al., 2009; Supèr et al., 2001; for reviews see Pasternak & Greenlee, 2005; Postle, 2006, 2015, 2016; Serences, 2016; Teng & Postle, 2021). As I will describe next, during the past two decades, a large body of evidence for the sensory recruitment hypothesis appeared in the literature, stemming from a variety of methodological approaches including behavioral and psychophysical experimentation, non-human primate studies, functional Magnetic Resonance Imaging (fMRI), and Transcranial Magnetic Stimulation (TMS).

Figure 1. 6: Simplified **e**xample of behavioral visual short-term memory tasks.

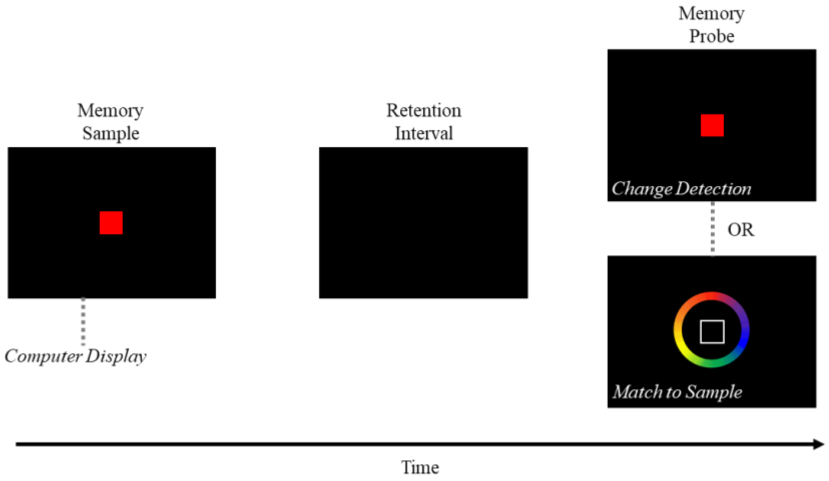


Fig.1.6. In order to study visual short-term memory, researchers design tasks which contain a memory sample, a retention interval and a memory probe. In change-detection tasks, participants indicate, usually with the press of a button, if the memory probe differs or not from the memory sample. In match-to-sample tasks, participants are required to match the memory probe to the memory sample.

1.3.1.1 Behavioral and Psychophysical Experiments

A number of behavioral and psychophysical studies provided evidence supporting the sensory recruitment hypothesis. Mainly, behavioral and psychophysical studies have focused on basic visual features (i.e., contrast, motion direction) and indicated that similar sensory mechanisms are involved in both visual perception and VSTM maintenance.

In detail, studies have indicated that VSTM maintenance involves different sensory feature-selective mechanisms, supporting that different stimulus visual features undergo different maintenance processes (Magnussen & Greenlee, 1999). For example, the maintenance of information in VSTM (for as long as 30 seconds), which share sensory-specific attributes processed by the SVC, such as spatial frequency (Magnussen & Greenlee, 1992) and orientation (Vogels & Orban, 1986) can be maintained with higher precision compared to texture (Harvey, 1986) and small spatial offsets (Fahle & Harris, 1992).

An additional example comes from findings that investigate the maintenance of color in VSTM. These findings showed that hue can be retained with great precision, thus supporting the involvement of brain regions regarding sensory processing of color in VSTM maintenance (Nilsson & Nelson, 1981). Moreover, one study provided evidence that color and spatial location are maintained in VSTM by separate systems (Vuontela et al., 1999). Vuontela et al. (1999) presented color or location distractors during the delay of a VSTM task, between two stimuli that differed in either color or spatial location. The retention of spatial location -but not color- was affected by location distractors, while color distractors interfered only with memory for color.

Numerous studies have supported the idea of feature-specific retention mechanisms in VSTM using irrelevant distractors or masks during the delay period of their VSTM tasks (Figure 1.7). Regarding spatial frequency, it has been shown that the range of interference by a masking grating with different spatial frequencies on delayed discrimination of retained spatial frequencies is comparable to the bandwidth of sensory masking or adaptation (i.e., larger interference on VSTM maintenance when retained and masked spatial differences ranged between 1-1.5 octaves; Magnussen et al., 1991). Further, this effect was unaffected by changes in the mask's orientation. This selective interference indicates that spatial frequency maintenance shares specialized mechanisms similar to those involved in perceptual processing (encoding) and differ from mechanisms involved in stimulus orientation.

Figure 1. 7: Simplified example of a visual short-term memory masking paradigm.

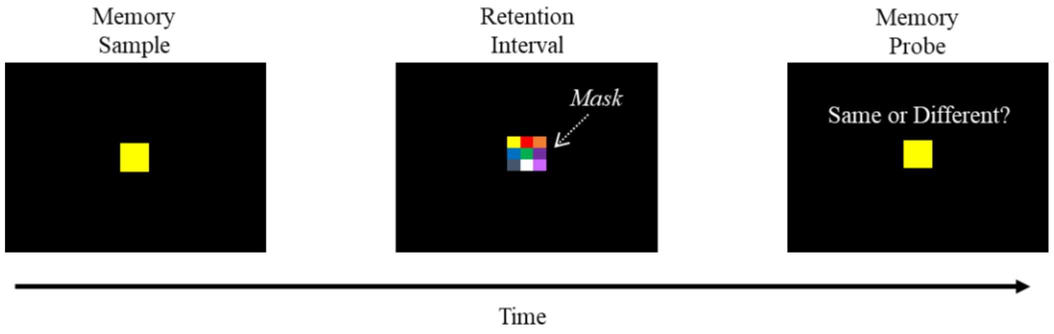


Fig.1.7. During the delay period of a visual short-term memory task an irrelevant mask is presented. In psychophysics the mask or an irrelevant distractor can be used to investigate the effects of specific perceptual processes on short-term memory retention.

Similar findings were reported for the selective maintenance of motion direction. In one study, monkeys were required to compare two moving stimuli (consisting of random-moving dots) separated by a delay period (Zaksas et al., 2001). The two comparison stimuli were spatially separated, and, during the delay, a random-motion mask was introduced in either the sample location or the location of the upcoming test. The effect of the mask was specific to its properties and location, indicating that when the spatial separation of two comparison stimuli was greater than a critical distance, there was an increase in the motion discrimination threshold. This critical spatial separation increased with retinal eccentricity, and its size coincided with the size of receptive fields in area V5/MT+, an area known to mediate sensory processing of motion in a retinotopic manner (e.g., Mundinano et al., 2019). Zaksas et al. (2001) findings, suggest that V5/MT+ might be involved in VSTM maintenance, thus supporting the idea that retinotopic visual cortex is involved in the storage of motion information.

These findings encouraged subsequent work, leading to additional compelling evidence that VSTM maintenance and perceptual processes share similar underlaying mechanisms. Recently, in a series of experiments, a study showed that the effects of VSTM load on detection sensitivity, are similar to the effects of perceptual load (Konstantinou & Lavie 2013). The authors of this study combined a delayed change-detection VSTM task with a visual search task that was presented during the delay period. They manipulated the visual load of the memory sample consisting of colored squares (either one square in the low load condition or six squares in the high load condition) or the perceptual load of the visual search task. Further, during the delay they presented an irrelevant stimulus in 50% of their trials, and participants were asked to detect whether the irrelevant stimulus was present or absent. Their results indicated that both increased VSTM and perceptual load impaired the detection of the irrelevant stimulus similarly. Notably, when the authors manipulated WM load using a successor naming task, the opposite effect was reported, where detection sensitivity of the irrelevant stimulus was increased.

Likewise, in a following study researchers explored the effects of VSTM load on selective attention, by presenting a visual search task that included either a congruent or incongruent distractor (Konstantinou et al., 2014). The visual search task was presented either simultaneously with the memory sample (during encoding) or during the delay

(VSTM maintenance). A congruency effect was reported, where the incongruent distractor had a greater impact on the visual search task when VSTM load was high, in both the encoding and maintenance conditions. Similarly with previous findings on detection sensitivity (Konstantinou & Lavie, 2013), Konstantinou et al. (2014) showed that the congruency effect was reversed when load was manipulated using a verbal WM task. Given that loading different WM systems led to opposite detection and congruency effects, and thus the effects cannot be attributed to generally higher cognitive load, these findings support that perceptual and memory processes share a similar neural architecture (Konstantinou et al., 2014; Konstantinou & Lavie, 2013).

Recent work provided insight for the mechanism behind these effects of VSTM load on selective attention. Particularly, a recent study fitted the contrast function on orientation discrimination while manipulating VSTM load (Konstantinou & Lavie, 2020). The contrast function can be used to understand the underlaying neural mechanisms of sensory areas by measuring attention changes in contrast responses (Pestilli et al., 2009). A horizontal shift of the contrast function, known as the contrast gain (Figure 1.8A), reflects contrast effects due to increased sensory input (e.g., Martınez-Trujillo et al., 2002; Schwedhelm et al., 2016), whereas a vertical shift, called response gain (Figure 1.8B), indicates exogenous influences irrelevant to the neural processing of contrast (McAdams & Maunsell, 1999; Treue & Trujillo, 1999). Konstantinou and Lavie (2020) combined a change-detection VSTM task with an orientation discrimination task, which was presented during the delay of the VSTM task. The memory sample consisted of either a low-load (one colored square) or high-load (four colored squares) array, and the orientation discrimination stimulus was randomly chosen in each trial from a set of eight contrasts (ranging between 0.1% and 90%). Before responding whether a memory probe was the same as or different from the memory sample, participants had to discriminate whether the orientation stimulus, which was presented outside the focus of attention, had a clockwise or anticlockwise orientation. When the researchers fitted the results of the orientation discrimination task to the contrast function, a rightward shift in the high-load condition performance compared to the low-load condition was observed, while no vertical changes were found between the high and low load conditions. These results describe the features of the contrast gain effect, supporting that the VSTM load effects on contrast are more likely due to increased sensory input (Konstantinou & Lavie, 2020), therefore similar underlaying mechanisms are shared between VSTM maintenance and perceptual processing of contrast.

Figure 1. 8: The contrast response function.

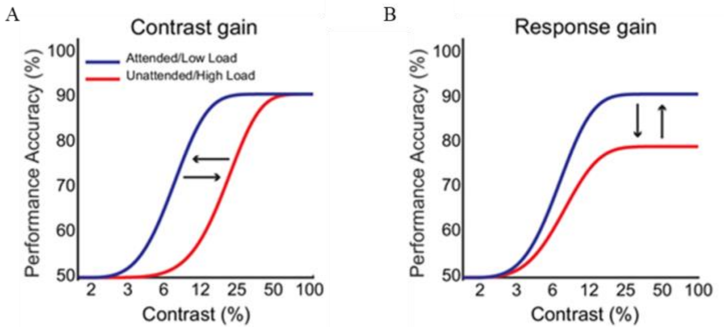


Fig1.8. The contrast response function. (A) Contrast effects due to increased sensory input lead to a horizontal shift of the function, referred to as "contrast gain". (B) Contrast effects due to exogenous influences cause a vertical shift, referred to as "response gain". Figure adapted from Konstantinou & Lavie (2020).

Further support for sensory feature-specific maintenance in VSTM was brought by another recent psychophysical study (Yörük et al., 2020), in which the authors explored the effects of perceptual visual crowding on VSTM maintenance. Because of the retinotopic nature of the SVC, perceptual visual crowding leads to an anisotropy deriving from online visual perception (Toet & Levi, 1992; see also Whitney & Levi, 2011), where radially centered targets (Figure 1.9A) are more prone to error than tangentially centered targets (Figure 1.9B). Yörük et al. (2020) tested if this perceptual effect is reflected in VSTM and showed that during a delayed orientation match-to-sample task, higher errors were reported for memory samples that were presented radially, as opposed to tangentially presented representations. Considering the retinotopic hallmark of crowding anisotropy, these results support the involvement of similar retinotopic processes by the SVC for both perceiving and retaining visual information.

Overall, the above psychophysical findings suggest that for specific visual features, the SVC employs similar neural mechanisms for both VSTM encoding (perception) and maintenance (memory). As I further discuss in Chapter 2, a hallmark of the sensory recruitment hypothesis is the shared neural substrate of perceptual and memory processes (for reviews see Lorenc et al., 2021; Pasternak & Greenlee, 2005).

Figure 1. 9: The effects of visual crowding on retinotopic cortex.

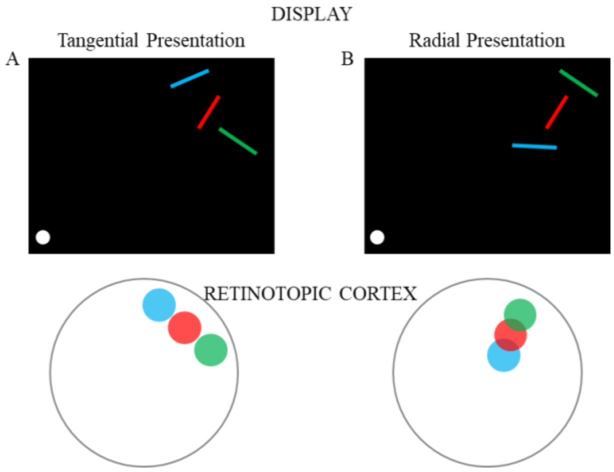


Fig.1.9. The crowding anisotropy due to the retinotopic nature of visual areas. (A) When the target (red line) is configured tangentially between other stimuli representations are less likely to retinotopically overlap. (B) A radial configuration of the target leads to increased overlap in the visual cortex.

1.3.1.2 Non-Human Primate Lesion and Electrophysiology Studies

The earliest evidence suggesting that pre-established brain areas (e.g., PFC) are insufficient to support VSTM alone, came from primate studies. Specifically, early electrophysiological studies focused on the inferotemporal cortex (IT), an area employed during the processing of complex shapes in an advanced stage of the visual stream (Ungerleider & Pasternak, 2004). These early findings showed that during VSTM tasks, the IT is capable of short-term maintenance of visual information (Chelazzi et al., 1993) and even presented evidence for selective neural activity separating perceptual and memory processes in the IT (Fuster, 1990; Miller et al., 1993). Moreover, lesion studies on primates proposed that frontal areas are not always required for the successful completion of a VSTM task (Petrides, 2000), as well as that their role in VSTM might in fact be more related to stimulus selection and attention rather than WM (Rushworth et al., 1997).

Subsequent studies provided evidence for the motion sensitive area V5/MT+ and its involvement in VSTM maintenance. In two studies (Bisley et al., 2001, 2004), monkeys were required to compare the direction of motion between two random-moving dot stimuli, presented sequentially between a 1500 ms delay. The results from these studies, indicated that microstimulation on V5/MT+ during the delay period resulted in a drop of VSTM performance (Bisley et al., 2001), and also that V5/MT+ neurons were active during the delay period of the VSTM task (Bisley et al., 2004). Such results were also replicated in a lesion study with a similar VSTM task, where monkeys with unilateral lesions on area V5/MT+, presented impairments in both the encoding and maintenance of motion stimuli (Bisley & Pasternak, 2000).

Further, in the early 2000s, came the first evidence associating electrophysiological correlates with activity in the primate area V1 of the SVC (Supèr et al., 2001). In this study, monkeys were trained in a delayed-response figure-ground segregation task in which a motion- or an orientation-defined figure was presented. After the delay, which varied between 0 ms to 2000 ms (0 ms, 500 ms, 1000 ms, or 2000 ms), monkeys were cued to make a saccade indicating the position of the previously presented figure. After analysing the contextual modulation reflected in the measured V1 neural activity (the subtraction of a neuron's response when background noise dots covered its receptive field from its response when the figure covered its receptive field), the authors reported that memory-related contextual modulation continued throughout the delay period of the VSTM task. This groundwork was essential for the formation of the sensory recruitment hypothesis.

Today, despite the ethical boundaries that greatly restrict primate experimentation, recent studies have provided similar evidence to that of Super et al.'s (2001) findings. In a recent study (van Kerkoerle et al., 2017), monkeys were trained to trace a curve that appeared before a memory delay, amongst distractors. After a 600 ms delay, the monkeys made a saccade to indicate the target curve. The authors measured SVC activity in the different layers of V1 and compared their results from the VSTM task to an attentional task (the same task without a delay). In an additional experiment, they included 50 ms masking stimuli during the delay period of their VSTM task, to examine the effects of visual masking on V1 activity. Van Kerkoerle et al. (2017), showed that similar V1 activity was measured during the attention and VSTM conditions, indicating a similar underlaying mechanism. Notably, layer specific measurements indicated stronger feedforward and feedback activity during the VSTM task compared to the attentional task. Further, even though decreased activity was measured during the presentation of masks, the representations could be later recovered. This was reflected by the late modulations in V1 activity during the delay period, which could predict the quality of the remembered curve, thus correlating VSTM performance with late V1 neural activity.

Non-human primate studies provided strong causal (lesion studies) and correlational (electrophysiological) evidence for the role of sensory areas in VSTM, and in part inspired the sensory recruitment hypothesis (e.g., Supèr et al., 2001). In the following section, I turn to fMRI evidence that supports the role of SVC in VSTM maintenance.

1.3.1.3 Functional Magnetic Resonance Imaging Studies

In order to correlate human neural activity with VSTM, studies have presented their VSTM tasks in the bore of the fMRI. As previously mentioned, two ground-breaking studies were able to decode memory related activity from the SVC, giving birth to the sensory recruitment hypothesis (Harrison & Tong, 2009; Serences et al., 2009). The novelty of these studies concerned the analysis of the fMRI data, which moved beyond the traditional measurements of blood oxygen level dependant (BOLD) activity signals (see Leavitt et al., 2017), and used trained classifiers to decode neural activity.

Harrison and Tong (2009) successively presented two sample gratings, followed by a cue indicating which of the two gratings' orientation should be memorised. A memory probe was then presented after an 11 second delay, consisting of a grating that participants indicated which way it was tilted relative to the remembered (cued) grating. In order to decode neural activity, the authors trained a classifier using data from the activity in areas V1-V4 of the SVC during the delay period. Using the trained classifier to test untrained data, they compared VSTM activity to the activity during passive viewing and indicated that activity patterns throughout the delay period in areas V1–V4 could successfully predict (> 80% classifier accuracy) the retained orientation of the orientation grating held in memory. Further, the pooled generalised performance activity across V1-V4 was significantly above chance, indicating that maintaining an orientation in VSTM involves similar orientation-selective neural populations as those that are activated when perceiving visual stimuli. Similar results were found in a VSTM task with a 10 second delay, which used both a color and an orientation change-detection task (Serences et al., 2009). In this study multivoxel pattern analysis revealed that activity patterns in V1 during the delay were feature-specific to the stored representation (color or orientation) and similar to that quantified during the discrimination of sensory input.

Beyond the above pioneering work (Harrison & Tong, 2009; Serences et al., 2009), subsequent studies presented evidence for increased BOLD activity in the SVC during VSTM. The first study to demonstrate this used a VSTM task, where the memory sample consisted of a cued colored circle within an array of four differently colored circles (Munneke et al., 2010). At the beginning of each trial, participants were instructed whether the maintained circle served as the memory set (VSTM condition) or as a location cue for an upcoming target stimulus (spatial attention condition). Following a five second delay, a set of four white circles with a left or right gap was shown. In the VSTM condition participants indicated whether a white circle was present in the memorized location and in the spatial attention condition participants indicated the side of the gap (left or right) of the white circle in the maintained location. The results of the study showed increased BOLD responses, which were retinotopically specific, during the delay period of the VSTM condition. In detail, the maintenance of spatial location in VSTM increased BOLD signal in the contralateral SVC (V1, V2 and V3), compared to the ipsilateral location, once again indicating increased activity in sensory specific visual information. Based on this work, a following study by Konstantinou et al. (2010), showed that activity in area V1 for a peripheral contrast stimulus presented during the delay of a change-detection VSTM task decreased when memory load was high (compared to a low load condition). This finding further supported that the SVC shares similar mechanisms for memory maintenance and perceptual encoding.

Further to this line of work, recent fMRI studies gave additional compelling evidence for the role of the SVC in VSTM. In one study, either one or six colored squares were presented in the memory sample and during a 3 second delay, participants were asked to report the presence (or absence) of a contrast increment which appeared in half the trials (Konstantinou et al., 2012). fMRI activity from the SVC during the delay, revealed that BOLD responses in areas V1, V2, and V3 decreased in the high VSTM load condition compared to when load was low, irrelevant to the presence of the contrast increment. However, an interaction effect between VSTM load and contrast increment presence was reported for BOLD activity in area V1. In detail, a higher suppression of V1 activity under the high VSTM load condition was found when the contrast increment was present, compared to when it was absent. The results of this study (Konstantinou et al., 2012) are in line with the authors’ previous work (Konstantinou et al., 2010, 2014; Konstantinou & Lavie, 2013, 2020), that show that the perception of contrast shares similar resources with memory representations in VSTM.

The abovementioned studies guided following studies, which in turn replicated previous findings and provided further insight for sensory recruitment during short-term visual information maintenance. In a delayed orientation match-to-sample task, Rademaker et al. (2019) presented either irrelevant distractors (white noise stimulus or oriented gratings in one experiment; faces or gazebos in a second experiment) or a blank screen during an 11 second delay period. The researchers trained a multivariate model, which unveiled that information about the remembered orientation was evident in all conditions in areas V1-V4. Further, in the oriented grating distractor conditions, the model could successfully decode the orientation of the distractor in areas V1-V4. These findings, further to decoding VSTM representation from areas V1-V4 of the SVC, indicate that memory and perceptual information may coexist in the SVC.

In another recent study, two orientation gratings were presented sequentially followed by a retro-cue (Christophel, Iamshchinina, et al., 2018). The retro-cue was used to prioritize one of the two gratings in memory; however, the cue had a 50% probability of being valid, meaning that in half the trials participants were tested on the non-prioritized remembered orientation. By training a model on the prioritized and non-prioritized conditions, the authors showed that prioritized representations could be successfully decoded in areas V1-V4, although no information about the non-prioritized representations was decoded in the SVC. Conversely, when the same data was reanalysed, representations for the non-prioritized representations were successfully decoded in the SVC (Iamshchinina et al., 2021). Specifically, in this reanalysis, Iamshchinina et al. (2021) retrained the model using data only from the prioritized representations. The new model could successfully detect activity from areas V1-V4 containing information about the non-prioritized orientation.

Lastly, one study investigated the effects of perceptual training on VSTM maintenance (Jia et al., 2021). During this study, participants performed an orientation change-detection task with an 11.8 second delay in the bore of the fMRI three times; once before perceptual training (pre-training), once following six days of perceptual training (post-training I), and once 10 days after perceptual training (post-training II). Jia et al.

(2021) showed that no differences in V1 BOLD activity were found between the trained and untrained orientations. However, their multivariate pattern analysis indicated that representations in V1 could only be decoded before perceptual training, since the classifier’s accuracy dropped to chance in both post-training phases. Despite the failure to detect V1 activity in the post-training phases, the authors reported that representations in V1 were still present, probably in a different neural state undetectable by fMRI. This conclusion was drawn by the authors given a second experiment they conducted using TMS (Experiment 2 of Jia et al., 2021; discussed below in section *1.3.1.4 Transcranial Magnetic Stimulation Studies*).

A lot of supporting evidence for sensory recruitment in VSTM comes from fMRI studies. Though, neuroimaging tools such as fMRI are limited to correlational inferences and may fail to accurately detect brain activity during brief cognitive processes (D'Esposito et al., 1999) such as VSTM. As I briefly discuss in later chapters (see Chapters 2 and 3), this correlational nature of neuroimaging techniques has -in part-contributed to the debate regarding the involvement of the SVC in VSTM.

1.3.1.4 Transcranial Magnetic Stimulation Studies

Numerous studies have employed TMS to understand the role of SVC during VSTM maintenance. As I discuss in section *1.4 Understanding Sensory Recruitment: The Value of Transcranial Magnetic Stimulation*, TMS is a reliable method to explore the neural architecture and the different neural mechanisms of VSTM. Given the extensinve focus of this thesis in TMS, a detailed description of TMS studies investigating the SVC in VSTM (including the studies included in this section) is presented in Chapter 2. Here, I will briefly present some of the most compelling TMS findings in support of the sensory recruitment hypothesis.

The first TMS study that supported the sensory recruitment theory was performed by Silvanto and Cattaneo (2010). In their study, Silvanto and Cattaneo (2010) investigated the role of the motion selective V5/MT+ area in VSTM. Participants performed a motion direction change-detection VSTM task, while reporting the presence and location of moving phosphenes. Results showed that overlapping phosphenes with the same direction as the memory sample, VSTM performance was impaired compared to a no TMS control condition and enhanced compared to when phosphenes overlapped but moved in the opposite direction to the memory sample. These results support a retinotopic involvement of area V5/MT+ in VSTM maintenance. Similar findings for area V5/MT+ were reported in a later study, which presented both facilitation and inhibition TMS effects for prioritized and unprioritized representations respectively (Zokaei et al., 2014).

Similar evidence to that of area V5/MT+ was shown in TMS studies investigating areas V1/V2 of the SVC. Van de Ven et al. (2012) showed that TMS during the delay period of a VSTM task impaired VSTM performance when memory load was high and TMS was delivered 200 ms into the delay period. Likewise, in another experiment, TMS delivered in the middle of the delay of a VSTM orientation match-to-sample task, resulted in impaired performance when stimulation matched the remembered-item's retinotopic location (Rademaker et al., 2017). Interestingly, Rademaker et al. (2017) showed that when stimulation was delivered on the ipsilateral retinotopic V1, VSTM performance was enhanced. Similar effects were found, when TMS was delivered early (100 ms) into the delay of a VSTM task (van Lamsweerde & Johnson, 2017).

Strong evidence in support of the sensory recruitment hypothesis came from a recent study, which investigated the effects of perceptual training in VSTM (Jia et al., 2021). In this study, TMS was applied on retinotopically localized V1 during the delay of an orientation change-detection task. Participants completed the task twice, once before and once after perceptual training and in both cases, TMS significantly impaired VSTM performance.

Despite the compelling evidence for sensory recruitment during retention -stemming from various experimental designs-, the role of the SVC in VSTM maintenance remains controversial. In the next section, I confer the controversies and briefly discuss why the sensory recruitment hypothesis is currently under debate.

1.3.2 The Sensory Recruitment Hypothesis Debate

Traditionally, studies exploring VSTM focused on measurements of sustained neural activity from neuroimaging tools (for a review see Leavitt et al., 2017). Under the scope of sustained neural activity, representations in VSTM are thought to be maintained online and are reflected in neural activity spikes (e.g., Chafee & Goldman-Rakic, 1998; Funahashi et al., 1989). Through vast research, such sustained neural activity has been noticed in both frontal (see Christophel, Allefed, et al., 2018; Funahashi, 2017; Levy & Goldman-Rakic, 2000; Riley & Constantinidis, 2016) and parietal (see Bettencourt & Xu, 2016; Ester et al., 2015, 2016; Xu & Chun, 2006) brain areas, making the role of these brain areas in VSTM maintenance undoubtable (for recent reviews see Christophel, Allefed, et al., 2018; Christophel et al., 2017; Lorenc & Sreenivasan, 2021; Postle, 2016; Serences, 2016; Xu, 2017, 2020).

The implementation of novel neuroimaging analysis methods that went beyond the traditional persistent activity view, generated numerous findings supporting the role of SVC in VSTM maintenance (described in section *1.3.1 Studying the Sensory Visual Cortex in Visual Short-Term Memory*), which gave rise to the sensory recruitment hypothesis (Harrison & Tong, 2009; Serences et al., 2009; Supèr et al., 2001; for reviews see Pasternak & Greenlee, 2005; Postle, 2006, 2015, 2016; Serences, 2016; Teng & Postle, 2021). Considering the evidence for sensory specific stimuli maintenance in VSTM, such as orientation (e.g., Harrison & Tong, 2009; Serences et al., 2009; Supèr et al., 2001), contrast (e.g., Konstantinou et al., 2010, 2012, 2014; Konstantinou & Lavie, 2013, 2020), and motion direction (e.g., Bisley et al., 2001, 2004, Bisley & Pasternak, 2000), the sensory recruitment hypothesis proposed that the SVC (i.e., areas V1-V4, area V5/MT+) has a dual function: (i) it is responsible for the precise sensory encoding of elemental visual features and (ii) the short-term maintenance of this information. Based on this proposition, SVC neurons are ideal candidates for storage because they exhibit highly selective tuning for specific visual features. Utilizing such a selective tuning, the involvement of the SVC in VSTM maintenance might be a highly efficient way to avoid recoding remembered information in other distal anatomical structures and to provide high VSTM fidelity cost-effectively. Moreover, this feature-specific selectivity of the SVC, which is critical for remembering subtle distinctions between stimuli, is absent in higher-order areas (see Postle & Yu, 2020 for a recent review). Despite the compelling evidence in favor of the SVC in VSTM, sensory recruitment for short-term information maintenance remains far from being established in VSTM.

Today, the sensory recruitment hypothesis is under debate (see Shevlin, 2020). Recent reviews explored evidence from behavioral, neuroimaging, TMS, and non-human primate electrophysiology studies in order to understand the contributing role of the

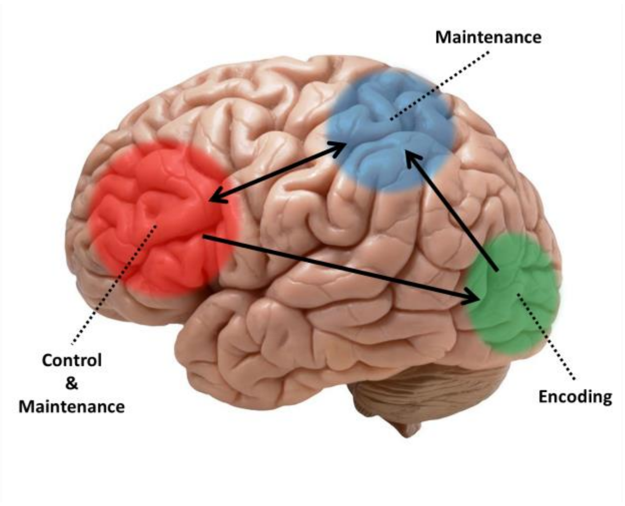
SVC during VSTM (Xu, 2017, 2020; see also Xu, 2018). Xu (2017, 2018, 2020) argued that contrary to the view that the selectivity of the SVC makes it ideal for storage, given the essential role of the SVC in visual information encoding (see Awh & Jonides, 2001; D'Esposito & Postle, 2015; de Graaf et al., 2014; Kammer, 2007; Masse et al., 2020; Serences, 2016; Shevlin, 2020), information maintenance by the SVC makes representations susceptible to overwriting as new stimuli are processed. Further, Xu (2017) pointed that SVC networks are not sufficiently wired to support the type of sustained activity thought to support VSTM. These reviews (Xu, 2017, 2018, 2020) concluded that the role of the SVC during VSTM strictly concerns the encoding of visual influx and that it does not contribute to the retention of visual information in short-term memory, since maintenance in VSTM is carried out mainly by the posterior-parietal cortex (PPC) and the PFC (Figure 1.10). Part of this conclusion was reached based on reviewed studies that showed minimal or no effects on VSTM performance when sensory interference (i.e., visual distractors or masks, TMS) was presented during the delay of VSTM tasks (Xu, 2017). The main argument against the role of the SVC and its involvement in VSTM maintenance (Xu 2017, 2018, 2020), derived from a study that was able to decode VSTM representations from activity patterns in the PPC but not from the SVC, when task-irrelevant distractors were present (Bettencourt & Xu, 2016).

Counterarguments regarding Xu’s (2017, 2018, 2020) conclusions attempted to reaffirm the sensory recruitment hypothesis (Gayet et al., 2018; Scimeca et al., 2018). In response to the overwriting susceptibility of SVC representations due to perceptual input, supporters of the sensory recruitment hypothesis, proposed that the SVC utilizes processes to protect representations, such as between layer top-down signals in area V1 (van Kerkoerle et al., 2017). These processes are similar to those employed by higher brain areas, such as the PFC, when differentiating mnemonic and perceptual information during attention modulation (e.g., Knight et al., 1999). Moreover, it has been postulated that instead of impairing VSTM, the interaction between memory representations and perceptual input might be beneficial. For instance, VSTM representations can bias perceptual input, thus improving perceptual continuity and goal-related behavior (Gayet et al., 2013; Kiyonaga et al., 2017). Regarding the role of sustained activity in VSTM, arguments in favor of the sensory recruitment hypothesis, discussed alternative explanations. Specifically, it has been argued that sustained activity in the PFC, might not in fact reflect VSTM representations per se, but instead echo a biasing signal to protect or direct attention towards goal related VSTM representations (Curtis et al., 2003; Sreenivasan & D'Esposito, 2019; Masse et al., 2020; Miller & Cohen, 2001; Sreenivasan et al., 2014).

Even though both sides of the debate present compelling evidence either for (e.g., Gayet et al., 2018; Scimeca et al., 2018) or against (e.g., Xu, 2017, 2018, 2020) the sensory recruitment hypothesis, the role of the SVC during VSTM maintenance remains an ongoing debate (Shevlin, 2020). This debate derives from a modular view of cognition (see Barack & Krakauer, 2021; Lorenc & Sreenivasan, 2021; Teng & Postle, 2021). The modular view seeks to understand the essentiality of the SVC in VSTM maintenance by asking *if* the SVC is necessary for the short-term maintenance of visual information, by means of the conventional persistent neuronal activity neuroimaging signature. As I describe next, recent views suggest that in order to achieve a better understanding of the neural underpinnings of WM, VSTM research should adopt a distributed view, and instead of asking *if*, start asking *how* the SVC contributes to VSTM representations.

Figure 1. 10: Maintenance of visual information in short-term memory according to Xu (2017).

Fig.1.10. According to Xu (2017), the sensory visual cortex (green) does not go beyond the encoding of visual information in visual short-term memory. Information maintenance happens mainly in the parietal-posterior cortex (blue) and the prefrontal cortex (red), which is also responsible for the top-down control of the memoranda.



1.3.3 A Distributed View: The Sensory Recruitment Framework

Today, WM is thought of as a flexible process, which can distribute representations depending on the available resources (e.g., Bouchacourt & Buschman, 2019; Oberauer & Lin, 2017; for a review see Buschman, 2021) and task demands (e.g., Ester et al., 2009; Reinhart et al., 2014; Tamber-Rosenau et al., 2015; for reviews see Christophel et al., 2017; D'Esposito & Postle, 2015; Franconeri et al., 2013; Lorenc & Sreenivasan, 2021; Serences, 2016). Further, numerous findings indicate that representations in WM are not only stored online through sustained neural activity, but also through activity-silent neural states, such as synaptic weight changes (e.g., Iamshchinina et al., 2021; Kozachkov et al., 2022; Lorenc et al., 2018; Rose et al., 2016; for reviews see Sreenivasan & D'Esposito, 2019; Masse et al., 2020; Lorenc et al., 2021; Lorenc & Sreenivasan, 2021; Teng & Postle, 2021). Influenced by these findings, and the distributed view of cognition (see Barack & Krakauer, 2021), researchers proposed that a better understanding of the SVC contributions to VSTM would emerge if the sensory recruitment hypothesis was no longer tested under a strictly modular view (Lorenc & Sreenivasan, 2021; Teng & Postle, 2021). For example, Xu's (2017, 2020) view that the SVC cannot by solely responsible for VSTM maintenance, is an extreme assumption under the modular view which can hardly be supported by modern cognitive neuroscience (Teng & Postle, 2021).

Under the scope of a distributed VSTM, sensory recruitment is viewed as a *framework*[2] rather than a *hypothesis* (Teng & Postle, 2021). The distributed view of VSTM suggests that representations are distributed across multiple brain areas (contrary to the modular view of single brain area maintenance) and are modulated by task related context and goals (Lorenc & Sreenivasan, 2021). Considering the latest evidence showing that capacity limitations, task demands, and different neural representation storage states influence WM maintenance (Christophel et al., 2017; D'Esposito & Postle, 2015; Franconeri et al., 2013; Lorenc et al., 2021; Lorenc & Sreenivasan, 2021; Masse et al., 2020; Serences, 2016; Sreenivasan & D'Esposito, 2019), the sensory recruitment framework suggests that to reach a coherent understanding of the SVC's involvement in VSTM, the focus should shift towards unveiling how information in SVC is stored and protected, how it interacts with other brain areas, and how it contributes to behavior (Lorenc & Sreenivasan, 2021; Teng & Postle, 2021). Put simply, the sensory recruitment framework proposes that instead of investigating whether the SVC is

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[2] From here on I will use the term *sensory recruitment framework* to refer to the SVC's potential involvement in VSTM maintenance, since currently it is deemed as more appropriate (Teng & Postle, 2021; see also Postle, 2021; Postle & Oberauer, in press).

essential for VSTM maintenance, research should focus on understanding the contribution of the SVC within the distributed brain network underlaying VSTM.

Hence, in order to reach a comprehensive understanding of sensory recruitment, in this thesis I aim to address the controversy for the role of the SVC in VSTM by utilising a methodology which can embody this distributed view (Barack & Krakauer, 2021; Krakauer, 2022). In the following section, I propose that a reliable method to understand the SVC contribution in VSTM is TMS.

1.4 Understanding Sensory Recruitment: The Value of Transcranial Magnetic Stimulation

In a hypothetical scenario, the most reliable way to investigate whether the SVC maintains visual representations, would be to completely inactivate the SVC during the delay of a VSTM task -after the encoding of a memory sample has been processed-, and reactivate it immediately before a memory probe is presented for comparison or matching (Figure 1.11; Scimeca et al., 2018). Despite this scenario being an ideal experiment, currently it can only remain hypothetical since it is impossible to be carried out. However, using non-invasive brain stimulation, such as TMS during the delay of a VSTM task, it is possible to approximate this experiment.

Figure 1. 11: Hypothetical scenario for investigating the role of the sensory visual cortex in visual short-term memory.

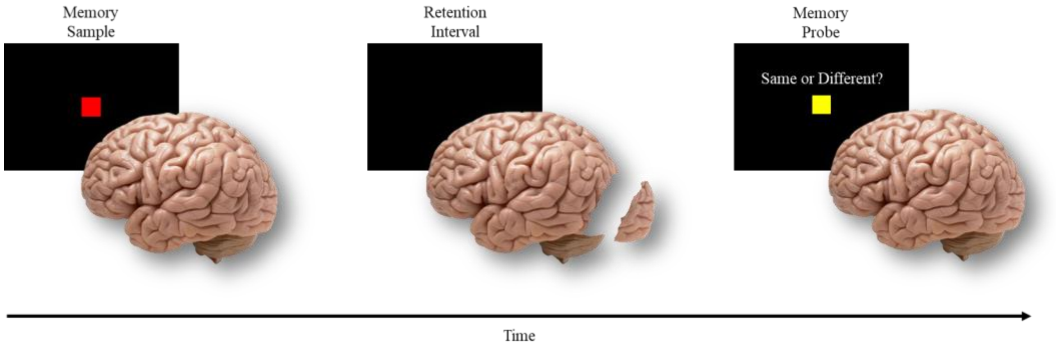

Fig.1.11. The most reliable way to understand whether the sensory visual cortex can maintain representations during visual short-term memory, would be to completely inactivate it during the delay (retention interval) of a visual short-term memory task.

1.4.1 Transcranial Magnetic Stimulation as a Reliable Tool to Explore Sensory Recruitment

TMS is a non-invasive method that uses a coil to deliver magnetic pulses that can interfere with neural activity in specific brain regions with good spatial and temporal resolution (e.g., the “virtual lesion” or “neural noise” methods; Harris et al., 2008; see also de Graaf, & Sack, 2011; Hallett, 2000; Pascual-Leone et al., 2000; Pitcher et al., 2020; Sack, 2006; Sandrini et al., 2011; Siebner et al., 2009) and has been shown to either inhibit brain processing or enhance neural excitability (e.g., Kim et al., 2015; Moliadze et al., 2003; Silvanto et al., 2018; for reviews see Robertson et al., 2003; Silvanto & Cattaneo, 2017). Thus, TMS can furnish causal information about the relationship between the brain network underlying behavioral responses, as opposed to the correlational nature of neuroimaging data (for recent reviews see Bergmann, & Hartwigsen, 2021; Pitcher et al., 2020). This gap between the correlational nature of neuroimaging data and the causal link of TMS, has been demonstrated since the introduction of TMS in cognitive science (for a review see Robertson et al., 2003). For example, initial neuroimaging evidence has led to the conclusion that the involvement of the pre-frontal cortex during sequence learning was required only after awareness for the sequence had been achieved (Clegg et al., 1998). It was only after the introduction of TMS in this line of work that the role of the pre-frontal cortex was established during the absence of awareness for sequence learning (e.g., Robertson et al., 2001). Similarly, the role of feedforward and feedback processes in area V1, remained controversial (e.g., Lamme et al., 2000), until Pascual-Leone and Walsh (2001) successfully applied TMS to interfere with back-projections between area V5/MT+ and V1.

Delivering TMS at the SVC has been shown to directly interfere with cortical activity during both perceptual (e.g., Tapia & Beck 2014; for a review see de Graaf et al., 2014) and memory processes (e.g., van de Ven & Sack, 2013; Zokaei et al., 2014), thus making the exploration of causal evidence plausible (de Graaf & Sack, 2011; Pitcher et al., 2020; Sandrini et al., 2011). Moreover, TMS has been shown reliable beyond activity-silent mechanisms (Rose et al., 2016) and it is thought to be a safe tool for healthy participants, as well as a valuable method for solving neuroscientific research questions (de Graaf & Sack, 2011; Hallet, 2000; Pascual-Leone et al., 2000; Pitcher et al., 2020; Sack, 2006). Therefore, comparably to the correlational nature of neuroimaging data, which is heavily reliant on the persistent neuronal activity (D’Esposito et al., 1999), TMS can furnish causal information about the relationship between brain activity and behavioral performance, making it a reliable tool to investigate the sensory recruitment framework debate.

Many studies have utilized TMS in an effort to present causal evidence for the involvement of the SVC during VSTM maintenance (see Chapter 2 for a detailed description of previous TMS studies). However, previous TMS studies provided mixed results, either for (e.g., Cattaneo et al., 2009) or against (e.g., van Lamsweerde & Johnson, 2017) the sensory recruitment framework. Further, studies have presented both inhibitory (e.g, Rademaker et al., 2017) and facilitatory (e.g., Cattaneo et al., 2012) effects on VSTM performance due to TMS interference. These controversial findings, possibly derive from methodological issues, that when properly addressed, TMS could provide a clear understanding of the causal link between the SVC and VSTM maintenance.

An example of such a methodological issue relates to the anatomical processing of visual stimuli within the visual field. In human visual system anatomy, when a visual stimulus is presented within 15° of visual angle in either the left or right visual field, it is perceived by the corresponding left or right temporal retina of the eye, and thus end up being processed by the ipsilateral V1 area (Figure 1.12A; see also Joukal, 2017; Wichmann & Müller-Forell, 2004). Further, within 15° of visual angle, the visual field of both eyes overlap (Figure 1.12B), and therefore visual information can be processed by both hemispheres’ V1(Joukal, 2017; Wichmann & Müller-Forell, 2004; see also Tong et al., 2006). This important fact about the neuroanatomy of the visual pathway, has been ignored by previous TMS studies (e.g., Rademaker et al., 2017; van de Ven et al., 2012), and, as described in Chapter 2 and with further detail in Chapter 3, could be a reason for the controversial findings regarding the sensory recruitment framework.

Figure 1. 12: The neuroanatomy of the human visual field.

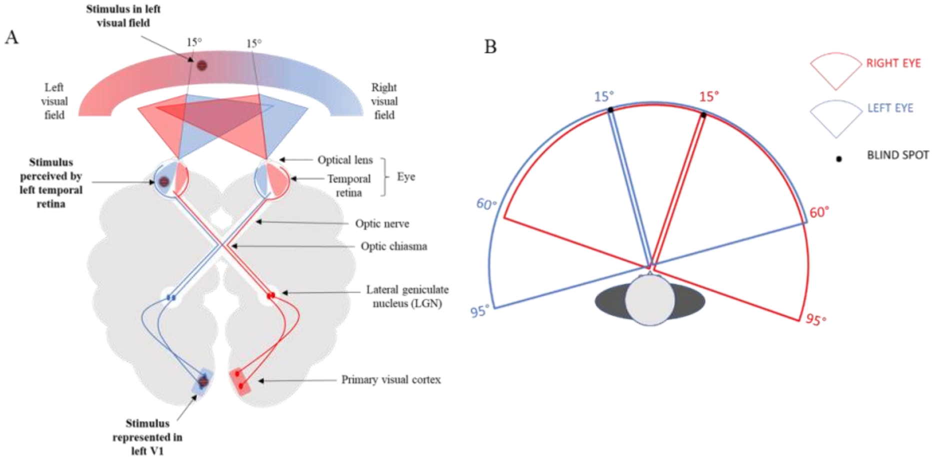

Fig.1.12. (A) A stimulus presented in the left visual field is perceived by the temporal retina of the left eye and is therefore represented only in the left (ipsilateral) V1 (B) Visual field angle of left and right eye. Stimuli presented within 15° of visual angle off of fixation are perceived by both eyes.

1.4.2 Transcranial Magnetic Stimulation of the Sensory Visual Cortex[3]

TMS on the SVC, such as on area V1, can evoke visual percepts, known as phosphenes. Phosphenes are the sensation of seeing light, without there being an external source of that light. If the TMS coil is placed on the SVC and stimulation is provided at adequate power, then phosphenes can be induced. This provides a functional method for localizing the SVC with TMS (Walsh & Pascual-Leone, 2003; see also section *4.2.1.4 Procedure* for a description of this method). Hence, TMS studies often rely on the induction of phosphenes as a SVC localization method or as a brain excitability heuristic. Subsequently, researchers have depended on the induction of phosphenes for both applied and basic research. For example, studies have used phosphene induction to understand brain excitability differences in migraine patients (Brigo et al., 2012), to test new technologies, such as transcranial focused ultrasound (Schimek et al., 2020), and to investigate the neural substrates of visual perception (de Graaf et al., 2014) and visual working memory (see Chapter 2).

However, it is not always possible to evoke phosphenes in human subjects using SVC TMS. This is reflected by the exclusion of participants in SVC TMS studies, due to the failure of reporting the experience of any visual percepts. This failure has been

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[3] A version of this subsection has been published elsewhere (see Phylactou, Traikapi, & Konstantinou, 2023)

attributed to various factors, such as the subjective nature of phosphene reporting, the lack of perceptual practice of participants, and differences in stimulation parameters (Kammer et al., 2005).

1.4.2.1 Phosphene Prevalence

Previous empirical studies, have provided numerous phosphene prevalence estimations, based on their experimental sample, with estimates of successfully inducing phosphenes ranging anywhere between 25% (Aurora et al., 2006) and 100% (van Lamsweerde & Johnson, 2017). Previous work has often reported that a common phosphene prevalence estimate is approximately 60% (Romei et al., 2008, 2012), however, this estimate was based on a single study with only four participants (Kammer et al., 2005). Yet, to the best of my knowledge there is no systematic estimate to date, that can inform TMS studies that aim to evoke phosphenes, as to the expected rates of successful and failed phosphene induction. Therefore, here, I systematically identified studies that used SVC TMS to evoke phosphenes, with the aim of determining the expected prevalence of successful phosphene induction and, respectively, the anticipated attrition rate.

After systematically searching the literature, I identified 95 studies that have used SVC TMS on healthy human participants, which also provided data regarding the success or failure of phosphene induction. In detail, following published guidelines (Page et al., 2021), I searched three databases (PubMed, Scopus, Web of Knowledge) to systematically identify possible TMS studies that stimulated the SVC and induced phosphenes. The search was restricted to the title and abstract. The specific search strings used in each database is presented in Table 1.1.

Table 1. 1: Search strings used in each database to identify eligible studies for phosphene prevalence.

Database	Search String
PubMed	((TMS[Title/Abstract]) OR (Transcranial Magnetic Stimulation[Title/Abstract])) AND (Phosphen*[Title/Abstract])
Scopus	TITLE-ABS-KEY (tms) OR TITLE-ABS-KEY (transcranial AND magnetic AND stimulation) AND TITLE-ABS-KEY (phosphen*)
Web of Knowledge	((TI=(TMS)) OR TI=(Transcranial Magnetic Stimulation)) AND TI=(Phosphen*) OR ((AB=(TMS)) OR AB=(Transcranial Magnetic Stimulation)) AND AB=(Phosphen*)

My search strategy yielded a total of 674 studies for initial screening. As illustrated in Figure 1.13, after excluding duplicates, I later screened titles and abstracts, which led to 209 potential studies for full-text screening. After full-text screening, 95 studies were deemed eligible to be included in my estimation model. The 95 identified studies together with their total sample size and the number of participants who perceived phosphenes are summarized in Table 1.2. These 95 studies provided data from a total sample size of 1939 participants, out of which 1435 have reported the successful experience of perceiving phosphenes.

To calculate the prevalence of phosphenes (θ) I used Bayesian estimation (Figure 1.14A). Specifically, I built a model that was informed by a Beta distribution with its parameters α and β set to 1, such that $\theta \sim \text{Beta}(\alpha = 1, \beta = 1)$. This prior distribution was chosen because it creates a uniform distribution, which means that equal probabilities are assigned to any possible prevalence percentage. Next, I calculated the binomial distribution for participants experiencing phosphenes (k), which was given by the probability θ for the total sample (n) in each study (i), which is expressed as $k_i \sim \text{Binomial}(\theta, n_i)$.

Figure 1. 13: The flow diagram followed for study identification.

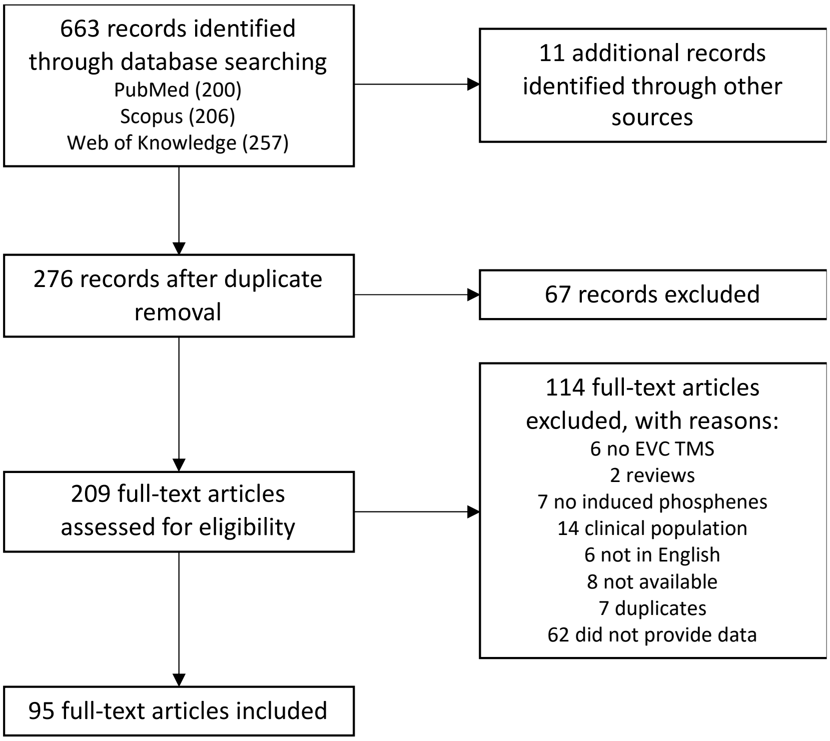


Fig.1.13. After screening 276 identified papers I have included 95 studies that induced sensory visual cortex transcranial magnetic stimulation and evoked

Following the model above, I was able to compute the posterior probability by implementing Markov chain Monte Carlo sampling. The posterior probability provided me with the estimated prevalence of phosphene induction (Figure 1.14B). The posterior probability had a mean of 0.74 (95% Credible Interval = [0.72, 0.76]). This reveals that approximately 74% of participants can perceive phosphenes and, respectively, a 26% attrition rate should be expected for TMS studies relying on phosphene induction. Put simply, it should be expected that one in four participants will fail to report reliable phosphene experiences.

Figure 1. 14: Bayesian estimation model used to estimate phosphene prevalence from 95 transcranial magnetic stimulation studies.

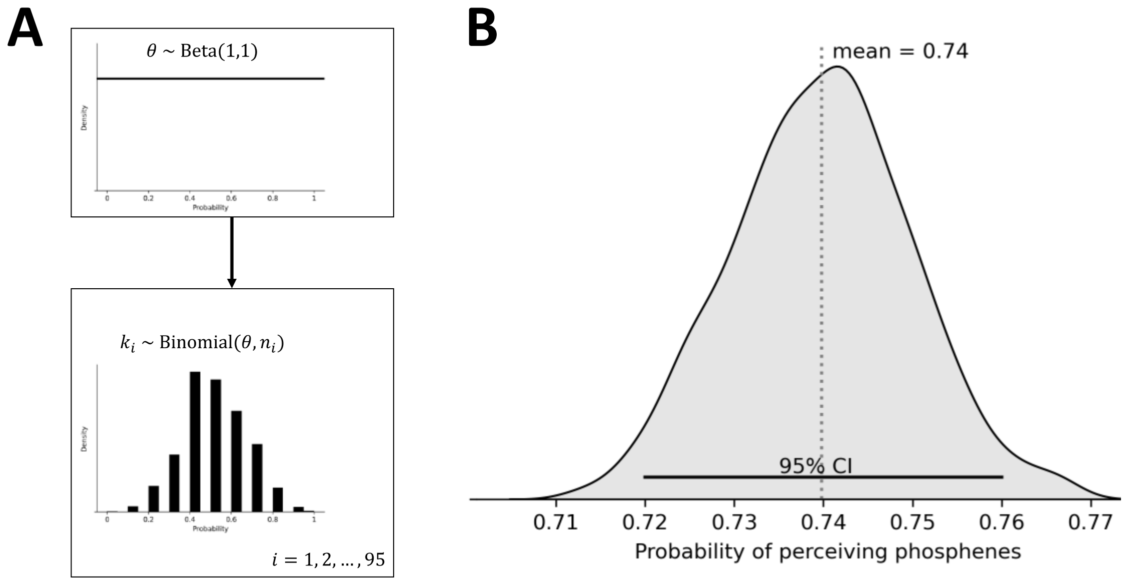


Fig.1.14. (A) The Bayesian model implemented to estimate the probability of perceiving phosphenes, and **(B)** the posterior probability that was computed by the model.

To date, and as far as I am conversant, this is the first systematic attempt to calculate phosphene prevalence. My findings revealed that one in four (approximately 26%) healthy participants will most likely fail to perceive any phosphenes during SVC TMS. This estimate is smaller compared to previous estimates (up to 40% failure in perceiving phosphenes), which were based on single studies with a small sample (e.g., 4 participants in Kammer et al., 2005).

Table 1. 2: The studies identified as eligible for calculating phosphene prevalence through the search strategy.

Article	Total sample size	Participants who perceived phosphenes	Percentage of perceiving phosphenes
Abrahamyan et al., 2011	10	10	100
Afra et al., 1998	27	25	92.5
Ambrosini et al., 2015	15	15	100
Antal et al., 2002	15	11	73.3
Antal et al., 2003a	22	9	40.9
Antal et al., 2003b	16	9	56.3
Aurora et al., 1998	11	3	27.3
Aurora et al., 1999	8	2	25
Aurora et al., 2003	10	3	30
Aurora et al., 2005	5	3	60
Bagattini et al., 2015	16	15	93.8
Bestmann et al., 2007	27	11	40.7
Bohotin et al., 2002	24	14	58.3
Boroojerdi et al., 2000	16	9	56.3
Boroojerdi et al., 2002	8	8	100
Brighina et al., 2002	15	7	46.7
Brigo et al., 2013	12	11	91.7
Brückner et al., 2015	48	40	83.3
Caparelli et al., 2010	12	6	50
Cengiz et al., 2022	16	13	81.3
Chota et al., 2021	25	18	72
Convento et al., 2013	12	8	66.7
Cowey & Walsh, 2000	6	6	100
Deblieck et al., 2008	27	21	77.8
Dugué et al., 2011	17	13	76.5
Fernández & Carrasco, 2020	18	16	88.9
Fernandez et al., 2002	19	18	94.7
Fierro et al., 2005	12	6	50
Filmer et al., 2013	34	29	85.3
France et al., 2006	18	12	66.7
Fried et al., 2011	23	23	100

Table 1.2 Continued

Gebrehiwot et al., 2021	15	10	66.7
Gerwig et al., 2003	32	30	93.8
Gothe et al., 2002	26	26	100
Gunaydin et al., 2006	30	21	70
Guzman-Lopez et al., 2011	12	10	83.3
Herpich et al, 2018	41	32	78
Höffken et al., 2012	50	33	66
Kammer & Baumann, 2010	10	10	100
Kastner et al., 1998	17	14	82.4
Keogh et al., 2020	37	32	86.5
Khammash et al., 2019a	28	20	71.4
Khammash et al., 2019b	30	23	76.7
Khedr et al., 2006	20	15	75
Knigth et al., 2015	25	16	64
Koivisto et al., 2017	12	5	41.7
Lou et al., 2011	19	19	100
Marzi et al., 2008	7	6	85.7
Mazzi et al., 2017	22	19	86.4
Mizuguchi et al., 2016	20	15	75
Mulleners et al., 2001	16	15	93.8
Oliveri & Calvo, 2003	10	10	100
Omland et al., 2014	32	25	78.1
Pearson et al., 2007	13	11	84.6
Phylactou et al., 2022	64	43	67.2
Rademaker et al., 2017	8	2	25
Rangelov et al., 2015	14	12	85.7
Ray et al., 1998	20	20	100
Renzi et al., 2014	10	10	100
Romei et al., 2007a	15	9	60
Romei et al., 2012	16	9	56.3
Romei et al., 2007b	15	10	66.7
Rothen et al., 2018	45	34	75.6
Saad & Silvanto, 2013	8	2	25
Saad et al., 2015	23	14	60.9

Table 1.2 Continued

Salminen-Vaparanta et al., 2012	8	7	87.5
Salminen-Vaparanta et al., 2011	20	10	50
Samah et al., 2017	17	10	58.8
Sander et al., 1996	14	5	35.7
Schaeffner & Welchman, 2016	30	12	40
Schimek et al., 2020	21	20	95.2
Seemungal et al., 2012	20	11	55
Silva et al., 2021	21	9	42.9
Silvanto et al., 2017	22	17	77.3
Silvanto & Cattaneo, 2010	12	9	75
Silvanto & Cattaneo, 2020	24	19	79.2
Silvanto & Muggleton, 2008	12	8	66.7
Silvanto & Soto, 2012	10	7	70
Siniatchkin et al., 2006	35	35	100
Siniatchkin et al., 2011	22	22	100
Soto et al., 2012	12	12	100
Sparing et al., 2007	10	6	60
Sparing et al., 2002	20	16	80
Sparing et al., 2005	19	10	52.6
Stewart et al., 2001	15	15	100
Strigaro et al., 2015	16	15	93.8
Tani et al., 2010	10	10	100
Tapia et al., 2014	110	87	79.1
Taylor et al., 2011	19	17	89.5
Taylor et al., 2010	27	12	44.4
Terhune et al., 2015	11	10	90.9
van de Ven et al., 2012	12	8	66.7
van Lamsweerde & Johnson, 2017	13	13	100
Webster & Ro, 2017	36	19	52.8
Zazio et al, 2019	15	8	53.3
Total	**1939**	**1435**	**74**

1.5 Research Overview

1.5.1 Rationale, Aim and Objectives

Evidence regarding the sensory recruitment framework remains controversial, resulting in an ongoing debate regarding the involvement of the SVC in visual information maintenance during short-term memory. Traditionally, the sensory recruitment framework has been investigated under the modular VSTM view, testing whether the SVC is essential or not for VSTM maintenance, with a heavy focus on the persistent neural activity measured in neuroimaging studies (Xu 2017, 2020). However, recent theories have proposed that research on the sensory recruitment framework should move beyond the modular view and towards a distributed view of VSTM. Through the distributed view, the sensory recruitment framework is explored based on the contributions of the SVC during VSTM maintenance within the brain network supporting WM (Christophel et al., 2017; Lorenc & Sreenivasan, 2021; Teng & Postle, 2021). Therefore, in this thesis, I focus on TMS, which is a reliable tool to explore the sensory recruitment framework, since it can overcome the limitations of neuroimaging data and the reliance on persistent neural activity during VSTM.

TMS is a reliable tool to investigate and produce rigorous findings regarding the sensory recruitment framework. In this thesis, I present a systematic review (Chapter 2) and meta-analysis (Chapter 3) of previous TMS studies, which have produced mixed results regarding the involvement of the SVC in VSTM maintenance (see Chapter 2). I propose that these mixed results stem from methodological issues, which when identified and properly addressed (Chapter 4), TMS combined with VSTM tasks can provide a comprehensive understanding of the involvement of the SVC during VSTM. Finally, to further understand the role of the SVC, I also implement memory load manipulations to explore the contributions of sensory resources during VSTM and whether sensory recruitment expands to the auditory modality (Chapter 5).

Therefore, the main aim of the current thesis is to gather evidence to explore the sensory recruitment framework. The general objectives and research questions of the current thesis are presented in Table 1.3. These objectives are further discussed in detail in each corresponding chapter.

Table 1. 3: General thesis objectives and research questions.

Chapter	Objective	Research Questions
2	• Systematically gather existing TMS evidence exploring the sensory recruitment framework. • Qualitatively review existing TMS evidence to explore the role of the SVC in VSTM and understand previous methodological issues.	i. Does the qualitative appraisal of previous TMS studies lead to a consensus for the role of the SVC dusting VSTM?
3	• Quantify results of previous studies to test the effects of SVC TMS during VSTM.	i. Does pooling results from previous studies together indicate an overall effect of SVC TMS during VSTM encoding? ii. Does pooling results from previous studies together indicate an overall effect of SVC TMS during VSTM maintenance? iii. Do the overall effects of encoding and maintenance differ?
4	• Address methodological oversights of previous studies to combine a VSTM task with TMS and explore the role of the SVC during VSTM.	i. Does TMS interference during the encoding phase of a VSTM task impair behvioral performance? ii. Does TMS interference during the maintenance phase of a VSTM task impair behavioral performance?
5	• Manipulate memory load to explore the effects of capacity limits on the detection of visual and auditory stimuli	i. Does increased VSTM load reduce the detection of a visual stimulus? ii. Does increased VSTM load reduce the detection of an auditory stimulus? iii. Does increased ASTM load reduce the detection of an auditory stimulus?

Notes. ASTM; Auditory Short-Term Memory; SVC; Sensory Visual Cortex, TMS; Transcranial Magnetic Stimulation, VSTM; Visual Short-Term Memory

1.5.2 Methodological Overview

The sensory recruitment framework remains an ongoing debate stemming from a modular view of cognition. Commonly, when such debates appear in the scientific literature, a reliable approach for reaching consensus, is through a rigorous review of the available literature (Mikolajewicz & Komarova, 2019). Consequently, previous studies attempted to review the available literature in order to address the sensory recruitment debate (e.g., Awh & Jonides, 2001; Christophel et al., 2017; D'Esposito & Postle, 2015; Ester et al., 2016; Lorenc & Sreenivasan, 2021; Serences, 2016; Sreenivasen et al., 2014; Tapia & Beck, 2014; van de Ven & Sack, 2013; Xu, 2017, 2020). However, none of these reviews used a systematic approach for study identification and inclusion, meaning that the studies included in these reviews were selected based on the authors' judgment (see Moher et al., 2009; Page et al., 2021). This can lead to intentional or unintentional exclusion of topic related studies. Further, these studies relied heavily upon qualitative reviews of the existing evidence, thus leaving any conclusions open to bias (see Gayet et al., 2018; Scimeca et al., 2018; Teng & Postle, 2021; Xu, 2018; see also Shevlin, 2020).

The next two Chapters of this thesis address these important omissions of previous review studies. In Chapter 2, I present a review of the existing literature of studies investigating the sensory recruitment framework using TMS. I propose that since TMS enables the exploration of causal evidence between cognition and its underlaying brain areas (de Graaf & Sack, 2011; Pitcher et al., 2020; Sandrini et al., 2011), identifying and reviewing the current state-of-the-art of SVC TMS studies during VSTM may provide insight regarding the ongoing debate on sensory recruitment. To address the issues found in previous reviews, in my review, the included studies have been systematically identified using pre-established guidelines (Moher et al., 2009; Page et al., 2021). Additionally, in order to overcome the bias of qualitative reviews, in Chapter 3, I have performed meta-analyses (Mikolajewicz & Komarova, 2019), in order to quantitively test the overall TMS effects of the included studies. To the best of my knowledge, this is the first review study to apply a systematic approach in study identification and perform meta-analyses, to explore the role of the SVC in VSTM maintenance.

The systematic review and meta-analyses, in addition to providing a more coherent understanding of the sensory recruitment framework, has several additional benefits (discussed in Chapter 3). One such benefit is that it allows to quantitatively explore the heterogeneity of the included studies (e.g., Higgins et al., 2003). Heterogeneity can be also explored through the systematic review (Chapter 2), to understand methodological issues in the current literature. In Chapter 4, I addressed the methodological issues of previous studies that have been identified by the systematic review, and I performed two TMS experiments, which tested and supported the causal involvement of the SVC in VSTM maintenance. In Chapter 5, I manipulate memory load and show that the SVC shares common neural substrates for both perception and memory, since exceeding VSTM capacity leads to reduces detection of visual, but not auditory stimuli. Lastly, I present a general discussion of the findings from Chapters 2-5, in the final Chapter 6 of this thesis.

1.6 Chapter 1 Summary

Traditionally, WM has been studied under the modular view, where specific brain areas are associated with a particular role in cognition. The modular view in the VSTM literature was heavily driven by neuroimaging evidence of persistent neural activity and established the involvement of brain regions, such as the PFC and PPC, during the short-term maintenance of visual information. However, the contribution of the SVC during VSTM maintenance, known as the sensory recruitment framework, remains debated. More contemporary theories propose a distributed view of VSTM, where the sensory recruitment framework should be investigated within the distributed brain network that supports VSTM, which includes various processes of neural storage beyond persistent activity, such as activity silent mechanisms (e.g., changes in the synaptic weights). Thus, the distributed view suggests understanding the various conditions under which enable the SVC to maintain information (or not), such as capacity limitations and neural-storage mechanisms, instead of simply whether it is essential for storage or not. Given that the sensory recruitment framework still remains controversial, and that the distributed view is a very recent introduction to the literature, this thesis aims to provide evidence for a coherent understanding of the role of the SVC during VSTM. I propose that a reliable tool to study the sensory recruitment framework is TMS. In the following chapter, I present the results of a systematic review of previous TMS studies investigating the sensory recruitment framework.

2 Sensory Recruitment in Visual Short-Term Memory: A Systematic Review of Sensory Visual Cortex Interference Using Transcranial Magnetic Stimulation

A version of this chapter has been published elsewhere (see Phylactou et al., 2022).

2.1 Chapter 2 Introduction

As thoroughly described in the previous chapter, it remains controversial whether the SVC is a necessary component of the network that underlies the short-term maintenance or storage of visual information. Further, it is well-established that VSTM is associated with frontal (Christophel, Allefed, et al., 2018; Funahashi, 2017; Levy & Goldman-Rakic, 2000; Riley & Constantinidis, 2016) and parietal (Bettencourt & Xu, 2016; Ester et al., 2015, 2016; Xu & Chun, 2006) brain areas. However, the role of the sensory visual areas (e.g., early visual areas such as V1, V2 or V5/MT+) in short-term maintenance of visual information is still unclear (e.g., Scimeca et al., 2018; Xu, 2017, 2020). Recent formulations of the debate focus on whether sensory visual areas are employed only during encoding of visual information (up to 200 ms after stimulus onset; Bays et al., 2011; Brady et al., 2016; Kammer, 2007; Vogel et al., 2006) or if they are also engaged during the short-term maintenance of such information (Konstantinou et al., 2012).

Central to this debate is the sensory recruitment framework, according to which activity in early visual areas is necessary for the successful maintenance of information in VSTM (Harrison & Tong, 2009; Serences et al., 2009; Supèr et al., 2001; for reviews see Pasternak & Greenlee, 2005; Postle, 2006, 2015, 2016; Serences, 2016). The sensory recruitment framework is supported by evidence from primate and human studies (e.g., Awh & Jonides, 2001; Christophel et al., 2017; Christophel, Iamshchinina, et al., 2018; Harrison & Tong, 2009; Lorenc et al., 2018; Pasternak & Greenlee, 2005; Postle, 2006; Rademaker et al., 2019; Serences, 2016; Serences et al., 2009; Sreenivasen et al., 2014; Supèr et al., 2001), suggesting that the SVC is not only involved in the encoding of visual information, but also in the successful maintenance of it. Yet, recent studies have provided evidence that irrelevant visual distraction has minimal impact on VSTM (Bettencourt & Xu, 2016; for recent reviews see Xu, 2017, 2020) suggesting that the SVC is not essential for the successful short-term maintenance of visual information (Ester et al., 2015, 2016; Lee et al., 2013; Mendoza-Halliday et al., 2014; Stokes, 2015; for a recent review see Riley & Constantinidis, 2016). Indeed, recent qualitative reviews of primate and human studies, suggested that the current evidence does not support the idea that the engagement of the SVC in the maintenance of visual information is required, but higher order cortical areas (i.e., prefrontal cortex and posterior parietal cortex) are most likely responsible for the short-term maintenance of visual information (Xu, 2017, 2020).

The role of the SVC during the encoding of information in VSTM is well studied (Awh & Jonides, 2001; D'Esposito & Postle, 2015; de Graaf et al., 2014; Kammer, 2007; Masse et al., 2020; Serences, 2016; Shevlin, 2020; Xu, 2017, 2020), and evidence from studies employing fMRI (e.g., Bettencourt & Xu, 2016), electroencephalography (EEG; e.g., Tcheslavski et al., 2018), brain stimulation (e.g., Lee et al., 2016) together with non-human primate studies (e.g., Lu et al., 2018) have linked activity in the SVC with successful encoding of visual information in VSTM. However, the role of the SVC in VSTM maintenance remains controversial. I suggest that this is due to methodological differences between relevant studies, such as maintenance periods that vary considerably between VSTM experiments from a few hundred milliseconds up to a few seconds (for a review see, van de Ven & Sack, 2013), and due to the fact that the neuroimaging methods employed for measuring such dynamic content-specific delay activity (i.e., fMRI and EEG) lack the precision to detect subtle or activity-silent processes (e.g., Rose et al., 2016; Stokes, 2015; see also Oberauer, 2019; Serences, 2016; Sreenivasen et al., 2014; for a recent review see Masse et al., 2020). These limitations, fail to exclude the possibility of SVC involvement even in tasks that show little or no sustained activity using fMRI during the maintenance period, making it unclear if in addition to its well-established role in encoding, SVC is also causally involved in the short-term maintenance of visual information.

Several previous attempts to reconcile disparate lines of evidence focused on qualitative reviews that lack a systematic approach of study identification, thus leaving any conclusions open to bias (Awh & Jonides, 2001; Christophel et al., 2017; D’Esposito & Postle, 2015; Ester et al., 2016; Gayet et al., 2018; Lorenc & Sreenivasan, 2021; Scimeca et al., 2018; Serences, 2016; Sreenivasen et al., 2014; Tapia & Beck, 2014;

Teng & Postle, 2021; van de Ven & Sack, 2013; Xu, 2017, 2018, 2020; see also Shevlin, 2020). Furthermore, most of these reviews relied heavily on neuroimaging data, which cannot provide causal information as to the question of whether the SVC is indeed a necessary component of the network that underlies the successful short-term maintenance of visual information (Masse et al., 2020; Serences, 2016; Sreenivasen et al., 2014; Xu, 2017; see also D'Esposito et al., 1999).

In the current chapter, I address these limitations by systematically identifying human studies that employed TMS. As previously mentioned (see section *1.4 Understanding Sensory Recruitment: The Value of Transcranial Magnetic Stimulation TMS*), I focus on TMS as it can furnish causal information about the relationship between brain activity and behavioral responses, as opposed to the correlational nature of neuroimaging data.

As discussed in detail below (see *2.2 Results*), previous TMS studies that aimed to explore the role of the sensory visual cortex during VSTM differentiated between the initial encoding-consolidation phases and the maintenance phase (e.g., Rademaker et al., 2017; van de Ven et al., 2012; van Lamsweerde et al., 2017; see also Xu, 2017). Specifically, the separation between encoding-consolidation and maintenance adopted in previous TMS studies is in line with evidence for a two-stage consolidation process in VSTM, which describes that, in order to store representations in VSTM, representations are initially allocated minimum resources in the early consolidation stage, but gradually receive more resources in a later consolidation stage if more encoding time is given (Ye et al., 2017, 2020). The second stage of information encoding and consolidation in VSTM might still take place for up to 200 ms after stimulus offset, due to memory load (e.g., Jolicoeur & Dell'Acqua, 1998; Vogel et al., 2006) and/or retinal persistence (e.g., Brockmole et al., 2002; Di Lollo & Dixon, 1988; see also Zhang & Luck, 2008; Ye et al., 2017, 2021). In line with this evidence, previous studies delivered TMS up to 200 ms after stimulus offset for testing the effects of sensory visual cortex TMS during VSTM encoding and consolidation, and for the effects of TMS on the maintenance phase of VSTM, TMS was delivered at least 200 ms after stimulus offset (de Graaf et al., 2014; Kammer, 2007; Masse et al., 2020; Serences, 2016; Shevlin, 2020; Xu, 2017, 2020, 2021; see also Brockmole et al., 2002; Di Lollo & Dixon, 1988; Ye et al., 2017, 2021). In line with this separation in previous TMS studies (Rademaker et al., 2017; van de Ven et al., 2012; van Lamsweerde et al., 2017) and the evidence that consolidation processes might still take place for up to 200 ms after stimulus offset (Brockmole et al., 2002; Di Lollo & Dixon, 1988; Jolicoeur & Dell'Acqua, 1998; Vogel et al., 2006; see also Ye et al., 2017, 2021), I grouped studies inducing TMS for up to 200 ms after stimulus offset in the VSTM encoding/consolidation phase (from here on referred to as encoding) and studies inducing TMS at least 200 ms after stimulus offset in the VSTM maintenance phase

2.1.1 Objective

To test the hypothesis that the SVC is a necessary component of the brain network that underlies the short-term maintenance of visual information, I performed, to the best of my knowledge, the first systematic review of the TMS literature. My specific aim was to systematically collect and appraise the studies that have investigated the role of the SVC in the encoding and maintenance of a delayed match-to-sample or a change detection VSTM task using TMS, in order to provide an interpretation of the disparate results.

2.2 Methods

2.2.1 Study Selection

A systematic search of three databases (PubMed, Scopus, Web of Science) was conducted according to published guidelines (Mikolajewicz & Komarova, 2019; Moher et al., 2009; Page et al., 2021). Data extraction was completed in March 2021 using the following thread: ((("visual short term memory" OR "vstm" OR "visual working memory" OR "short term memory" OR "working memory")) AND ("primary visual cortex" OR "sensory recruitment" OR "sensory recruitment hypothesis" OR "early sensory cortex" OR "early visual cortex")) AND ("transcranial magnetic stimulation" OR "tms" OR "behavioural" OR "behavioral" OR "brain stimulation" OR "visual mask" OR "manipulation" OR "reaction time" OR "reaction times" OR "accuracy"). Since this was the first attempt to systematically gather such evidence, the search was conducted without chronological limitations and applied within all fields of the databases. Additionally, studies were identified through previous review papers (Awh & Jonides, 2001; Christophel et al., 2017; D'Esposito & Postle, 2015; Serences, 2016; Sreenivasen et al., 2014; Tapia & Beck, 2014; van de Ven & Sack, 2013; Xu, 2017, 2020).

Following the PRISMA statement (Moher et al., 2009) for systematic reviews and meta-analyses, 14 articles matched the criteria and were included in the systematic review. Details of the final literature search are presented using a PRISMA flow diagram in Figure 2.1. The literature search was conducted using the following thread:

Figure 2. 1: Systematic review and meta-analyses PRISMA statement.

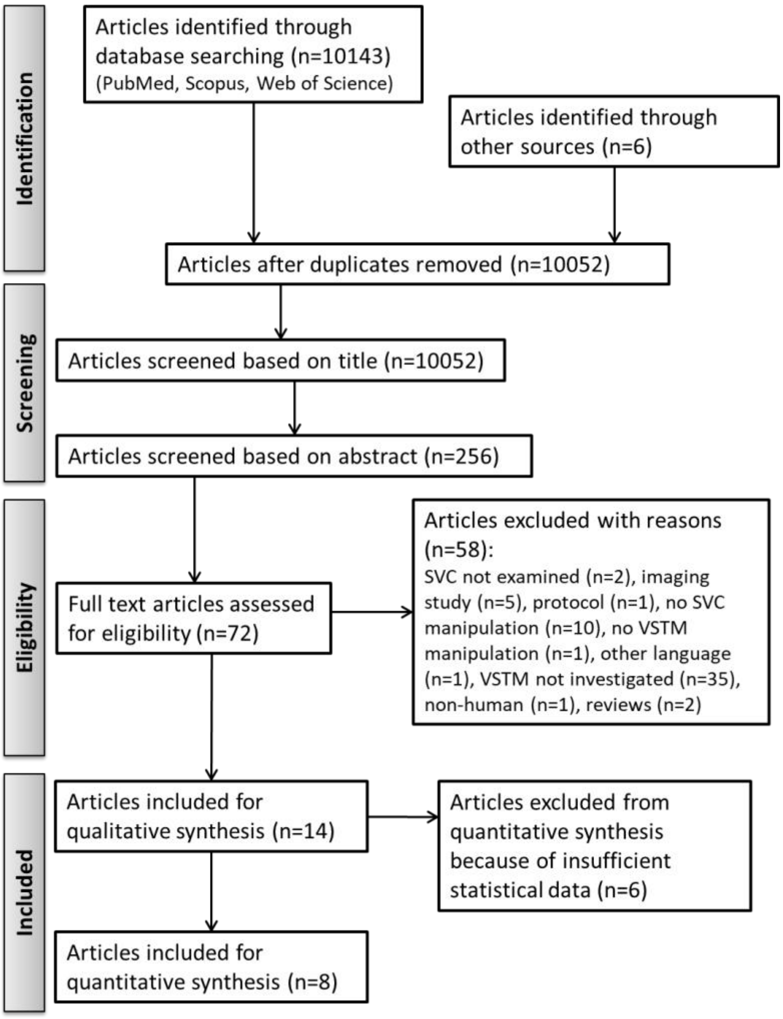


Fig.2.1. The PRISMA flow diagram followed for the systematic review and meta-analyses as suggested by Moher et al. (2009). Screening and eligibility assessment were completed by two independent researchers. SVC; sensory visual cortex, VSTM; visual short-term memory.

2.2.2 Inclusion and Exclusion Criteria

Three inclusion criteria were determined to identify eligible studies: (1) behavioral measures of VSTM performance (i.e., accuracy, absolute error, percent correct, precision, guess rate and signal detection), (2) causal interference of the SVC using TMS during a VSTM task, and (3) human participants. In addition, two exclusion criteria were defined which included: (1) any form of mental or physical pathology and (2) reports written in a language other than English. No age limitations were set for my search, however the identified studies solely included adults.

2.3 Results

The systematic search of the literature led to the identification of 14 papers. These papers included a total of 18 experiments that interfered with SVC activity using TMS during a VSTM task. A total of 248 individuals participated in the 18 experiments. Short descriptions of the included studies and their experiments are presented in Table 2.1.

2.3.1 Methodological Issues

A number of methodological issues such as the different apparatuses used (i.e., stimulator, coil), targeting methods (e.g., neuronavigation, phosphene induction), as well as the different output settings (e.g., power, frequency, number of pulses) have been identified (de Graaf & Sack, 2011; Pitcher, et al., 2020; Sadrini, et al., 2011) as factors that can possibly affect the homogeneity of the experiments (van de Ven & Sack, 2013). In the studies considered here, TMS stimulation was delivered with a 70 mm figure-of-eight coil in all experiments. The majority of experiments (*n* = 16) targeted area V1, while two focused on V5/MT+. Eight of the included experiments aimed to directly investigate the role of the SVC in VSTM. The remaining six studies had different aims, but nevertheless reported behavioral outcomes whilst interfering with TMS on the SVC during a VSTM task, making them useful for the purposes of this systematic review and meta-analysis. In eight of the included experiments, TMS output power was determined using the functional method of eliciting phosphenes (see Walsh & Pascual-Leone, 2003), while in the remaining ten a fixed TMS power output was used. When interfering with the SVC, two experiments delivered TMS in four pulses,

Table 2. 1: Articles systematically identified to be included in the systematic review and meta-analysis.

	Article	Description	ROI (pulse)	Targeting (output power)	VSTM Task	Control	TMS temporal point (after stimulus offset)	N	Behavioral measure
1	Cattaneo et al. (2009)	SVC role in mental-imagery and short-term memory	V1 (sp)	Phosphene induction (65% of Magstim 200 stimulator)	Time Memory or imagery task	No TMS & vertex TMS	**Exp1:** 2000 ms **Exp2:** 0 ms	**Exp1**: 14 **Exp2:** 14	Accuracy
2	Silvanto et al. (2010)	SVC role in VSTM	Right or left V5/MT + (sp)	Phosphene induction (120% of phosphene threshold)	**Exp1:** motion speed detection task	Ipsi- /contra- & No TMS	3000 ms	9	Accuracy
3	Cattaneo et al. (2012)	SVC role in mental imagery	V1 (3p)	2cm above inion (60% of Magstim SuperRapid stimulator)	**Exp2:** Time imagery task	No TMS & vertex TMS	1000 ms	10	Accuracy
4	Soto et al. (2012)	SVC role in attentional guidance by priming and working memory	V1 (3p)	2cm above inion (90% of phosphene threshold)	Priming detection task, with working memory task	Sham TMS	1700 ms	12	Accuracy
5	Silvanto et al. (2012)	Subliminal perception interference in memory	V1 (3p)	Phosphene induction (90% of phosphene threshold for n=7, 50% of Medtronic MagPro R 30 stimulator for n=3)	**Exp1b:** Orientation change detection task	Sham TMS	1000 ms	**Exp1b**: 10	Detection sensitivity
6	van de Ven et al. (2012)	SVC role in VSTM	Right or left V1 (sp)	(1) Phosphene induction for n=8 (2) Neuronavigation for n=5	**Exp2:** Non-natural shape change-detection task	Ipsi- /contra-	100 ms, 200 ms or 400 ms	12	Detection sensitivity

(110% of phosphene threshold)

Table 2.1 continued

7	Saad et al. (2013)	Effects of external visual input in internal representations	V1 (5p)	2cm above and .5cm laterally from the inion towards the right hemisphere (45% of a Nexstim stimulator)	**Exp2:** Orientation change detection task **Exp3:** Shape change detection task	Sham TMS	**Exp2:** 2000 ms or 5000 ms **Exp3:** 2000 ms	**Exp2:** 16 **Exp3:** 8	Accuracy
8	Zokaei et al. (2014)	Effects of TMS depending on representation state in VSTM	V5/MT + (4p)	fMRI localization (60% of Magstim Rapid^2 stimulator)	Motion match to sample task	**Exp1:** low power TMS **Epx2:** Low power TMS & Vertex TMS	**Exp1:** 3100 ms **Exp2:** 300 ms after first or second memory array	**Exp1:** 13 **Exp2:** 17	Precision
9	Malik et al. (2015)	SVC role in trans-saccadic memory of features	Right and left V1 (3p)	Neuronavigation (60% of N/A stimulator)	**Fixation task:** VSTM orientation change detection task	Ipsi-/contra- & no TMS	250 ms	8	Percent correct
10	Saad et al. (2015)	Difference in VSTM and imagery neural bases	V1 (5p)	(1) Neuronavigation for n=N/A (2) Phosphene induction for n=N/A (90% of phosphene threshold for n=N/A or 65% of Magstim Rapid^2 stimulator for n=N/A)	Orientation change detection task	Sham TMS	2600 ms	15	Detection sensitivity

Table 2.1 continued

11	Koivisto et al. (2017)	TMS effects on quality of memory representations	Right and left V1 (sp)	Neuronavigation (65% of Nextim eXimia^{tm} stimulator)	VSTM orientation match task	**Exp1:** Ipsi-/ contra- & no TMS **Exp2:** Ipsi-/ contra- & no TMS	**Exp1:** -30 ms to 120 ms (30 ms intervals) **Exp2:** 120 ms, or 150 ms, or 180 ms	**Exp1:** 12 **Exp2:** 7	(1) Proportion of guessing (2) Precision
12	Rademaker et al. (2017)	SVC role in VSTM	Right or left V1 (3p)	Neuronavigation (80% of phosphene threshold)	VSTM orientation match task	Ipsi-/contra- & Sham TMS	0 ms or 900 ms	8	(1) Absolute error (2) Precision (3) Guess frequency
13	van Lamsweerde et al. (2017)	SVC role in VSTM	Right V1 (sp)	Neuronavigation (110% of phosphene threshold)	**Exp3:** color match to sample task	**Exp3:** ipsi-/ contra-	**Exp3:** 0 ms, 100 ms, or 200 ms	**Exp3:** 21	(1) Absolute error (2) Precision (3) Guess frequency (4) Swap errors

14	Jia et al. (2021)	Training role in VSTM representations	Right or left V1 (5p)	Retinotopic Mapping (60% of Magstim Rapid^2 stimulator)	**Exp2: orientation change detection task**	**Exp2:** Sham TMS	**Exp2:** 1500 ms	**Exp2:** 20	Accuracy

Notes. 3p; three pulses, 5p; five pulses, Exp; experiment, ROI; region of interest, sp; single pulse, TMS; transcranial magnetic stimulation, VSTM; visual short-term memory four in five pulses, six delivered three-pulse TMS, and six experiments delivered a single TMS pulse. Moreover, eight experiments targeted the SVC in only one hemisphere.

In all experiments, control conditions were used to compare with possible effects in the TMS conditions. These controls differed between the experiments. Despite the fact that in seven experiments there were control conditions where no TMS was applied at all, other control conditions were also included to account for the noise and haptic artefacts of the stimulation. In particular, within these seven experiments, three additionally compared SVC stimulation with vertex stimulation. The remaining four stimulated only one hemisphere and therefore used the ipsilateral -to the stimulation region of interest (ROI)- visual hemifield condition as a control (compared to the contralateral one). In two experiments, an ipsilateral visual hemifield condition was used as the only control, while in six experiments control was solely a sham TMS condition. One experiment used both an ipsilateral visual hemifield and sham TMS condition as controls. In the remaining two experiments, one used a low (ineffective) TMS output power as a control, while the other used both low powered TMS and vertex TMS.

The inconsistency between the methods used leads to two important issues. Firstly, the lack of a specific TMS protocol to be followed in a certain field of research can produce mixed or misinterpreted results (de Graaf & Sack, 2011; Sadrini, et al., 2011). Second, it does not support reproducible science, and in the case of a meta-analysis, could lead to significant heterogeneity (see van de Ven & Sack, 2013). Taken together, these findings highlight the wide variability of methods (e.g., stimulation parameters) used to study TMS interference as an important factor in why the role of SVC in VSTM still remains unclear.

2.3.2 Transcranial Magnetic Stimulation During Encoding

The effects of TMS interference of the SVC activity during the encoding phase of visual information was tested in six experiments, from five studies (Cattaneo et al., 2009; Koivisto et al.,2017; Rademaker et al., 2017; van de Ven et al., 2012; van Lamsweerde & Johnson, 2017). As expected, the majority of these studies presented evidence supporting the involvement of the SVC during VSTM encoding.

Cattaneo et al. (2009) used TMS to interfere with SVC during a visual imagery task or a VSTM task. Participants were presented for 1 second with either an analog time which they had to remember (VSTM task) or a digital time, of which they had to imagine and remember the analog form (visual imagery task). Stimulation was applied at 0 ms after stimulus offset, at the beginning of a 2 second delay period, which is typically considered the encoding phase of VSTM (Bays et al., 2011; Brady et al., 2016; Kammer, 2007; Vogel et al., 2006). Participants then had to respond whether a dot would fall within or outside the remembered clock-hands. Accuracy and reaction times were compared between the SVC TMS condition, a no-TMS control condition, and a vertex TMS control condition. Reaction times were significantly slower during the SVC TMS conditions in the VSTM task, compared to the two controls, indicating an impairment in the performance of a VSTM task as a result of TMS during the encoding phase, therefore supporting the involvement of the SVC in VSTM encoding.

Subsequent studies reported experiments that provide further evidence for the involvement of the SVC in VSTM encoding using more sensitive statistical methods, such as mixture models (see Grange et al., 2021). Koivisto et al. (2017) conducted two experiments to investigate whether TMS affects precision or guessing rates in a VSTM task, and whether these are affected dichotomously (‘all or nothing’) or gradually. The orientation of a remembered Landolt-C presented for 12 ms (or 24 ms for n = 1) had to be matched to a probe presented after a 1 second delay period. In the first experiment TMS was delivered at -30, 0, 30, 60, 90, and 120 ms relevant to the onset of the stimulus and in the second experiment at 120, 150, and 180 ms after stimulus onset. The proportion of guess trials and the precision in the task were compared between the ipsilateral and contralateral conditions, as well as with a no-TMS control condition. The results showed higher guessing rates across both experiments in the contralateral TMS condition between 60 and 150 ms demonstrating the effects of TMS interference in the SVC during the encoding phase of VSTM.

Koivisto et al. (2017) provided evidence supporting the involvement of the SVC during VSTM encoding through their paradigm, even though their research objectives differed from the ones of this systematic review. Following these sensitive statistical methods, some studies, which directly investigated the role of the SVC during VSTM encoding, provide additional support for its involvement. Rademaker et al. (2017) asked participants to match the orientation of one out of four gratings which were presented for 200 ms in four visual field quadrants corresponding to either the same, ipsilateral, contralateral, or diagonal TMS ROI. TMS was delivered either at the beginning (0 ms after stimulus onset) or midway during a 2 second delay period (900 ms, see section TMS interference during maintenance for further details) of the VSTM task and a sham TMS condition was also used as control. The authors reported more errors when stimulation matched the remembered-item location compared to when the remember-item location was furthest to the stimulation. Also, early stimulation had a significantly stronger effect compared to late stimulation. Additionally, higher precision was measured when the pulse and target overlapped (same and ipsilateral conditions) compared to when they were far apart (diagonal condition) and guessing was reported higher when TMS was earlier than later.

Similarly, participants in an experiment by van Lamsweerde and Johnson (2017) had to remember the color of three squares presented for 150 ms. A probe presented after a 1 second delay period asked them to match the color of one of the three remembered squares. During the VSTM task, TMS was induced at 0, 100, or 200 ms after stimulus offset. As previously discussed, encoding processes take place up to 200 ms after stimulus onset, therefore, even though van Lamsweerde and Johnson (2017) considered their 100 ms (after stimulus offset, thus 250 ms after stimulus onset) condition reflective of encoding processes, using the above criterion I will discuss the 100 ms and 200 ms conditions in the TMS interference during maintenance section. Their results indicated that guess rates were higher when TMS was applied at stimulus onset in the contralateral condition. Swap rate effects (an indication of recalling a non-cued item) were also reported, which were significantly decreased in the contralateral compared to the ipsilateral condition. Further, a significant interaction of TMS and side (ipsilateral/contralateral) was reported on precision, with the effect seeming stronger at earlier TMS timing conditions. Given the stronger effects at earlier TMS timing conditions, similar to Koivisto et al. (2017) described above, the authors concluded that TMS effects are evident during memory encoding, but are no longer effective once consolidation in VSTM has been achieved.

Van de Ven et al. (2012), found no effect on the performance in a VSTM task when SVC TMS interfered during encoding at 100 ms after stimulus onset but did find an interference effect at 200 ms post stimulus onset. Participants performed a change detection task on a sample of either one (low load condition) or three (high load condition) non-natural shapes presented for 150 ms and maintained in VSTM during a 1.5 second delay period. Participants had to respond whether a probe was the same or different as the memory sample and accuracy of change detection was measured using signal detection theory. During the delay period, TMS was induced at 100 ms, 200 ms, or 400 ms after the memory set onset. A significant effect was found only in the 200 ms high load condition (described further in the TMS interference during maintenance section), which led the authors to the conclusion that the SVC's involvement in VSTM mainly takes place during the early maintenance phase.

In summary, the findings of the studies described above indicate that, apart from the experiment reported by van de Ven et al. (2012), all five remaining experiments reported a TMS effect on behavioral performance during the encoding phase of a VSTM task indicating that the results from studies using TMS to interfere with the SVC during the encoding phase of VSTM are consistent with the well-established role of the SVC in VSTM encoding. Next, I turn to the evidence from human TMS studies examining the involvement of SVC in short-term maintenance.

2.3.3 Transcranial Magnetic Stimulation During Maintenance

TMS was delivered during the maintenance phase of a VSTM task (i.e., more than 200 ms after stimulus onset) in 14 experiments from twelve different studies (Cattaneo et al., 2012; Jia et al., 2021; Malik et al., 2015; Rademaker et al., 2017; Saad & Silvanto, 2013; Saad et al., 2015; Silvanto & Cattaneo, 2010; Silvanto & Soto, 2012; Soto et al., 2012; van de Ven et al., 2012; van Lamsweerde & Johnson, 2017; Zokaei et al., 2014). As discussed in detail below, although the majority of these studies provide evidence supporting the sensory recruitment framework, others either failed to find such evidence or their findings are more consistent with an interaction between perceptual and VSTM processes, as I suggest below.

Silvanto and Cattaneo (2010) investigated the role of the motion selective V5/MT+ area in VSTM. The VSTM task consisted of two successively presented moving stimuli, which had either a right or a left direction and were presented at two different speeds. In each condition, the two stimuli were presented for 300 ms each and moved at different directions, but at the same speed. A cue followed the stimuli presentation and informed participants which of the two stimuli should be maintained; 3 seconds into the 5.5 second delay period, TMS was delivered to area V5/MT+. Next, participants had to subjectively rate the location and direction of movement of the phosphene before being presented with a probe stimulus. The probe had the same direction as the memory sample and participants were asked to report whether the speed of the last motion stimulus was faster or slower than the memory sample. The authors reported that when moving phosphenes overlapped and had the same direction as the moving stimuli, memory accuracy was significantly lower compared to the no TMS condition and higher compared to when phosphenes overlapped but moved in the opposite direction to the stimuli. These results indicate that, further to the involvement of the SVC during VSTM maintenance, area V5/MT+ maintains visual memory representations in a retinotopic manner.

The involvement of area V5/MT+ in VSTM maintenance was further supported in two experiments by Zokaei et al. (2014). In the first experiment participants were asked to remember two motion stimuli presented above and below fixation for 200 ms. The color of each stimulus was either red or green and one color was probed. Participants had to match the movement direction of the remembered stimulus to that of the probe. During the 3.7 second delay period of this task, participants were also asked to identify, after being probed with a color, if the same-colored stimulus was above or below fixation. After 3.2 seconds into the delay period, TMS was delivered, followed by the memory probe. In the second experiment, the two motion stimuli, instead of being presented together, were sequentially presented for 300 ms each and each was followed by a 1 second delay period. TMS was applied 300 ms after the onset of either the first or the second stimulus. Following the second stimulus, a colored probe appeared indicating to participants to match its direction to that of the same-colored motion stimulus's direction. A low intensity TMS condition was used in both experiments as a control condition and a vertex TMS condition was additionally introduced in the second experiment. The results of the first experiment showed that in the ineffective TMS condition there was a significant impairment in performance between congruent (if the position identification task probe matched the color of the memory task probe) and incongruent (if the position identification task probe did not match the color of the memory task probe) conditions which disappeared in the effective TMS condition. Similarly, in the second experiment, a significant impairment in precision was found in the low TMS condition when the first stimulus was followed by TMS, compared to when the second stimulus was followed by TMS; this effect was not evident in the high TMS condition. The authors described this as a facilitation effect of TMS, explaining that non-privileged memory items (i.e., memories in the incongruent trials; see Hitch et al., 2020) were likely suppressed and thus enhanced by stimulation. Since TMS can enhance neural excitability, in addition to inhibiting brain processing (Robertson et al., 2003), this facilitation effect is consistent with the findings of Silvanto and Cattaneo (2010) suggesting the involvement of area V5/MT+ during VSTM maintenance.

In addition to the involvement of area V5/MT+, TMS evidence for the involvement of early visual areas V1/V2 was provided in the studies discussed below. Cattaneo et al. (2012) applied TMS on area V1 of the SVC during the delay period of a VSTM task. In the task, participants were presented with a digital time for 1 second and had to remember the equivalent analog clock-hands. At the beginning of each trial, an adaptor was used that either overlapped with the to-be-remembered clock-hands or not. TMS was delivered 1 second after stimulus onset and at the end of a 700 ms delay period, participants responded whether a dot fell within or outside the remembered clock-hands. Results of the participants' accuracies indicated that the adapter decreased performance in the no-TMS and vertex-TMS control conditions, but the adapter's effect disappeared in the SVC TMS condition. Similar to Zokaei et al. (2014), a facilitation effect of the TMS was found, which suggests that, similarly to area V5/MT+, early visual areas V1/V2 are also involved in VSTM maintenance.

A recent study by Jia et al. (2021), studying the effects of perceptual training in VSTM, provided strong evidence in support of the sensory recruitment framework for area V1. Specifically, they used an orientation change detection task, where participants had to remember the orientation of one grating presented for 200 ms, and report whether a probe presented after a 4 s delay period had a clockwise or counterclockwise tilt compared to the remember stimulus. TMS was applied 1.5 s into the delay period. Participants completed the task twice, once before and once after perceptual training. In both cases, TMS significantly impaired accuracy in the VSTM task.

Additional evidence for the role of areas V1/V2 was found by van de Ven et al. (2012) (also described above in the section TMS interference during encoding), during SVC stimulation in two different conditions throughout the 1.5 second delay period, at 200 ms and 400 ms after stimulus onset (as well as at 100 ms corresponding to encoding; discussed in the previous section). TMS affected task performance in the contralateral compared to the ipsilateral condition only in the high load 200 ms TMS condition. These findings support the involvement of the SVC in the maintenance of visual information, mainly during the 200 ms window. Likewise, in Rademaker et al.'s (2017) study (also described previously; see TMS interference during encoding section), the SVC was stimulated 900 ms into the delay period of their VSTM task. As discussed previously, more errors were reported when stimulation matched the remembered-item location compared to when the remember-item location was furthest to the stimulation and higher precision was reported when TMS and target overlapped (same and ipsilateral conditions) compared to when they were further apart (diagonal condition). Taken together these results indicated that stimulation that overlapped with the same or ipsilateral visual field affected task performance when compared to the visual field that was further apart. However, it should be noted that these results were larger for earlier (during encoding) rather than later (during maintenance) stimulation. Similar evidence was shown in van Lamsweerde and Johnson's (2017) work (also discussed previously; see TMS interference during encoding section), whose results showed a significant interaction of TMS and side (ipsilateral/contralateral) on precision, with the effect seeming stronger at the 100 ms after stimulus offset TMS timing condition. On the same line with van de Ven et al. (2012) and Rademaker et al. (2017), van Lamsweerde and Johnson's (2017) effects were stronger during their 0 ms and 100 ms, rather than their 200 ms condition, suggesting that the SVC is involved in the earlier stages of VSTM.

Further to the inhibitory and facilitatory effects of TMS during VSTM maintenance, two studies discussed an interaction of TMS between perceptual and memory processes. Silvanto and Soto (2012) studied the intervention of subliminally perceived visual items in the SVC. In Experiment 1b TMS was applied over the SVC during a VSTM task. Participants were instructed to remember the orientation of a grating presented for 200 ms over a 2 second delay period. In the majority of the trials (66%), a low contrast distractor appeared 1 second into the delay period for 13 ms, which was either congruent (same) or incongruent (different) from the memory sample. TMS was also induced 1 second into the delay period and sham TMS was used as control. The results indicated that when there was no distractor present (remaining 34% of trials), SVC TMS impaired the ability to detect the probe difference but facilitated this ability when the distractor was incongruent compared to the sham TMS condition. The authors explained these results as a possible perception and memory mechanisms interaction, where TMS possibly enhanced neurons in a suppressed state at the incongruent distractor condition, thus making it easier to perceive.

In a similar manner, an interaction between perception and memory processes was discussed by Saad et al. (2015), who investigated the differences between imagery and VSTM neural bases. In their VSTM condition, participants had to memorize the contrast of a grating presented for 300 ms throughout a 4 second delay period. SVC TMS was applied 2.6 seconds into the delay period, and the delay was followed by a probe grating for which participants had to indicate whether it had a higher or lower contrast compared to the remembered one. The probe could either be slightly or more noticeably different in contrast than the remembered, thus introducing a harder or easier condition, respectively. A sham TMS condition was used to allow for comparisons. Additionally, during different blocks of the experiment, participants were asked to either create a mental image of the remembered stimulus (imagery condition) or not (VSTM condition). Results indicated that SVC TMS enhanced detection sensitivity relative to sham TMS in both the imagery and VSTM conditions. However, when it came to reaction times, SVC TMS only had an effect in the VSTM condition compared to sham, where reaction times were found to be slower. In line with previous studies (Cattaneo et al., 2012; Zokaei et al., 2014), the enhancement of detection sensitivity by stimulation in the VSTM and imagery tasks were discussed as TMS facilitatory effects. The difference found in reaction times between the VSTM and imagery conditions, was attributed to perceptual processes, where in the memory condition, the noise added by TMS possibly affected the time needed to gather perceptual evidence to judge in the discrimination task.

Silvanto and Soto (2012) and Saad et al. (2015), further to supporting the involvement of the SVC in VSTM maintenance, reported an interaction between perception and VSTM. A similar interaction was noticed in two other studies, despite the fact that no other inhibitory or facilitatory TMS effects were found to support the involvement of the SVC in VSTM maintenance. Soto and Silvanto (2012) combined a priming task with a memory task in order to investigate attentional guidance. Participants were cued whether they should remember (VSTM task) or just look (priming task) at a colored circle, which was presented for 200 ms. In the VSTM task, after an individually adjusted delay period, a probe appeared and participants had to respond whether it was the same or different circle as the memory sample one. TMS was delivered at area V1 1 second after the memory sample onset. At 1 second during the delay period, along with the TMS, a search task asked participants to identify which of two circles had a horizontal gap and report whether the gap was on the left or right side. In the priming task, no memory probe was shown after the search task. No effects on VSTM performance were found between the TMS and a sham-TMS condition but the effects of TMS for the priming search task were significantly modulated by memory requirement. Specifically, participants responded more accurately in the search task in the TMS condition but only when memory was required. In line with the previously mentioned studies (Saad et al., 2015; Silvanto & Soto, 2012) these effects indicate an interaction of TMS with perceptual processes, modulated by what is maintained in memory.

Similar results were found in a group of experiments by Saad et al. (2013), where they examined how the tilt aftereffect can affect memory representations. In two of their experiments, SVC TMS was applied during a VSTM task. In the VSTM condition of the first experiment participants were requested to remember the orientation of a grating and in the second experiment the color and size of one square. In both cases, the memory sample was presented for 300 ms and was maintained during a 5.3 second delay period, which was followed by a same-sized adapter grating, that had either the same or a 20-degree tilt difference (in the same direction) from the memory sample. In the first experiment, TMS was delivered either at 2 or 5 seconds into the delay period. In the second experiment, TMS was delivered only at 2 seconds into the delay period. In the VSTM conditions, a probe appeared after the delay period where participants had to report the change from the memory sample (first experiment) or match it to the memory sample (second experiment). Results showed no difference between TMS and a sham TMS control condition on the memory task, however the tilt aftereffect, was significantly decreased by TMS in the memory condition (compared to a passive one).

Similarly to the results of Soto and Silvanto (2012), the tilt aftereffect, which is a perceptual process, was modulated by memory requirements, indicating once more an interaction between perceptual and memory processes.

Even though the majority of studies showed either a direct TMS effect or a perception and VSTM interaction effect due to TMS, one study failed to find any evidence in support of the sensory recruitment theory. Malik et al. (2015) investigated the role of the SVC across trans-saccadic remembered features and used a VSTM TMS paradigm in one of their experiments. Participants had to remember the orientation of one grating presented for 100 ms and then report the difference in direction between the remembered one and a probe grating (i.e., clockwise or anticlockwise). TMS was induced 200 ms after the start of a 900 ms delay period. Comparisons were made between the contralateral and ipsilateral TMS ROI to visual hemifield condition, as well as in comparison to a no TMS condition. No differences were found, which, according to the authors, is consistent with previous evidence that TMS delivered over the SVC does not interfere in low VSTM load conditions, for example, when only one item has to be maintained (van de Ven et al., 2012).

Taken together, the results from the systematic review on TMS interference during memory maintenance indicate that the SVC is likely involved in VSTM maintenance, supporting the sensory recruitment framework. This is reflected in all but one of the studies by the direct TMS effects on memory performance and the TMS interaction effect between perception and VSTM. Following the description of the included studies, below, I summarize the results of the systematic review regarding the role of the SVC in VSTM.

2.3.4 Systematic Review Summary

The majority of the described studies indicated a likely involvement of the sensory visual cortex in both the encoding and maintenance phase of VSTM. However, the results provided by the identified studies, especially those applying TMS during the maintenance phase of VSTM, reflect some issues likely deriving from the variety of methodological approaches used between the studies.

Regarding VSTM encoding, all but one study (van de Ven et al., 2012) provided evidence in support of the role of the sensory cortex. The lack of such an effect in the

100 ms condition of the van de Van et al. (2012) could be due to a number of methodological issues. Specifically, van de Ven et al. (2012) used two different localisation methods and found a significant difference in the variable of interest (significantly different A' under the higher load condition of their experiment, which was the only condition reported to have significant results) between the participants depending on which localisation method group they belonged to. Furthermore, since comparisons were made between the memory load condition and the TMS timing, it is likely that a TMS effect actually does exist in both conditions (i.e., TMS affected memory performance in both load conditions). For example, no additional control condition (e.g., sham or no TMS) was used other than the ipsilateral visual hemifield of the targeted ROI. Therefore, because of the lack of dichoptic stimulus presentation (see Carmel et al., 2010), it remains possible that encoding of the visual information was in fact processed by the sensory visual cortex in both hemispheres (Tong et al., 2006; Zhao et al., 2021) and thus the effect remained undetected when comparing the ipsilateral versus the contralateral condition of the experiment.

Another issue reflected in the results of the included studies, concerns the fact that some studies provided evidence of inhibitory TMS effects (Jia et al., 2021; Rademaker et al., 2017; Silvanto & Cattaneo, 2010; van de Ven et al., 2012; van Lamsweerde, & Johnson, 2017), while others reported facilitatory TMS effects (Cattaneo et al., 2012; Saad et al., 2015; Zokaei e al., 2014) on VSTM performance. Examining the methodological differences between these studies, a possible explanation of this contradiction could lay in the distinct stimulation power output used for TMS. Specifically, it has been reported that lower TMS outputs can often lead to facilitation effects, while suprathreshold intensities are needed in order to disrupt activity and behavior (Kim et al., 2015; Moliadze et al., 2003; Silvanto et al., 2018; see also Silvanto & Cattaneo, 2017). In the current systematic review, studies showing facilitation effects utilized a standard TMS output for the majority of their participants, while the rest used an individualized threshold. Alternatively, the mixed inhibitory and facilitatory TMS effects might unveil a different TMS interference effect between distinct storage mechanisms. For example, TMS could in some cases interfere with active neural representations, thus inhibiting performance, whereas in other cases TMS can facilitate activity that is close to baseline (see Robertson et al., 2003; Rose et al., 2016; Silvanto & Cattaneo, 2017). In line with this alternative explanation, it has been recently postulated that VSTM might employ a variety of processes to protect visual representations (Lorenc et al., 2018, 2020) and that these contradictory TMS effects might reflect the use of different storage mechanisms (Adam et al., 2021; Silvanto & Cattaneo, 2017).

The majority of the TMS studies investigating the involvement of the sensory visual cortex during VSTM maintenance reported evidence supporting the sensory recruitment hypothesis. However, four experiments described in three different papers reported no direct significant effects of sensory visual cortex TMS on memory performance (Malik et al., 2015; Saad, & Silvanto, 2013; Soto & Silvanto, 2012). A closer look at the experiments that did not report any TMS effects unveils an interesting common denominator. Specifically, all four experiments presented only one stimulus that was ought to be remembered. In fact, in the fixation task experiment by Malik and colleagues (2015), which was designed as a control condition for their main research objectives, the authors reported that no significant results were expected, since sensory visual cortex TMS in such low load conditions has been previously found to be ineffective (van de Ven et al., 2012). In the two experiments reported by Saad et al. (2013), no effect was found when sensory visual cortex TMS was compared to a sham condition. Though, further analyses indicated that TMS was more effective during the VSTM task when compared to a passive condition (with no memory maintenance requirement). Likewise, no effects were reported in the work of Soto and Silvanto (2012) on VSTM performance between the TMS and sham conditions. However, effects by sensory visual cortex TMS in their priming task, were significantly modulated by whether memory maintenance was required or not.

This interaction between perceptual and memory mechanisms, as well as the role of processing load, have been identified and reported in other sensory visual cortex TMS studies (Saad et al., 2015; Silvanto & Soto, 2012; van de Ven et al., 2012). This interaction has also been supported by behavioral studies, which suggested that the perception of visual stimuli and VSTM are underlaid by shared neural mechanisms (Magnussen et al., 1991; McKeefry et al., 2007). Furthermore, the VSTM load and perceptual performance relationship has been previously studied, indicating that VSTM capacity load can affect both performance and sensory visual cortex activity (Konstantinou, et al., 2012, 2014; Konstantinou, & Lavie, 2013, 2020). In fact, the sensory recruitment hypothesis stems from this shared neural substrate between perception and VSTM (Pasternak, & Greenlee, 2005), which is reflected in dual and distraction tasks (for a recent review see Lorenc et al., 2021). Thus, a possible explanation for the failure to detect a TMS effect in these experiments is low sensory visual cortex neural demands (i.e., perceptual and/or memory load). For example, studies have indicated that the maximum number of visual objects that can be maintained in VSTM is estimated to range between three and four items (Cowan et al., 2005; Luck, & Vogel, 1997; Todd, & Marois, 2004; Vogel, et al, 2001, 2005; Vogel, & Machizawa, 2004). Therefore, if this is reflected in the sensory visual cortex's activity, it is possible that enough resources were still available in the sensory visual cortex due to low load VSTM task demands, thus, TMS noise leaves the maintained representations unaffected (see de Graaf, & Sack, 2011). It could be argued that in some cases, where only one stimulus was presented, a strong TMS effect was found (Jia et al., 2021). However, some methodological differences could explain why Jia et al. (2021) were able to show an effect despite the sensory load. Specifically, in the Jia et al. (2021) study, an orientation stimulus combined with retinotopic mapping was employed, which allowed researchers to identify and stimulate specific V1 areas which correspond closely to the neurons processing the stimulus orientation.

Additionally, another methodological issue that likely contributes to the debate, relates to the stimulus complexity used for the memory array in VSTM tasks. It has been reported that sensory visual cortex is involved in the maintenance of elemental visual features such as orientation and direction of movement (Harrison & Tong, 2009; Serences et al., 2009). However, when stimuli complexity increases, different brain regions might be recruited for encoding and maintenance, such as the intraparietal sulcus (Xu & Chun, 2006; Xu, 2007) and the posterior parietal cortex (Song & Jiang, 2006). Therefore, in studies using complex stimuli (e.g., van de Ven et al., 2012), the neural processes required for successfully maintaining visual information in VSTM might involve higher order brain areas in addition to sensory visual cortex (Teng & Postle, 2021). This might result to null effects when TMS is applied over sensory visual cortex during the memory delay since such representations might be protected through a distributed VSTM network (Lorenc & Sreenivasan, 2021; see also Gayet et al., 2018; Scimeca et al., 2018).

Overall, the systematic review provides additional evidence for the well-established role of the sensory visual cortex in VSTM encoding, by identifying and summarizing the relevant TMS studies. Further, the systematic review of TMS studies supports the involvement of the sensory visual cortex during VSTM maintenance. It is suggested that the contradictory results derive from the variety of methods utilized, such as the binocular presentation of stimuli, the storage mechanism of VSTM representations, the memory and perceptual load, and the memory stimulus complexity. Next, I turn to a biref discussion of these qualitative findings.

2.4 Chapter 2 Summary

The causal evidence that was systematically reviewed here, derived from the TMS studies investigating the role of the SVC in VSTM, seem to be support my hypothesis that SVC is a necessary component of the brain network that underlies both the encoding as well as the short-term maintenance of visual information, in line with the sensory recruitment framework (Awh & Jonides, 2001; Christophel et al., 2017; Pasternak & Greenlee, 2005; Serences, 2016; Sreenivasen et al., 2014). Further to the well-established involvement of the SVC during the encoding of visual information in VSTM, results from numerous TMS experiments indicate that the role of the SVC goes beyond this initial encoding phase and is also involved in the maintenance of memory representations. Even though some studies failed to detect a TMS effect, an interaction between perception and VSTM was evident, a finding that supports a possible shared neural mechanism between perception and VSTM in the SVC.

Previous qualitative reviews that studied the sensory recruitment framework remain inconclusive and open to interpretation. Here, I aimed to systematically identify and review studies that have investigated the role of the SVC in VSTM using TMS, a method that allows exploration of causal relationships. Fourteen studies were identified and qualitatively reviewed. The results from the systematic review indicate that the SVC is likely involved in both the encoding and maintenance phase of VSTM. I suggest that in some cases where evidence did not show significant effects of TMS, this is due to low memory load or low perceptual task demands. Further, I noted that the role of binocular stimulus presentation and stimulus complexity might contribute to the controversial findings.

Even though most TMS studies included in this systematic review seem to support sensory recruitment, the qualitative assessment of these studies is still susceptible to bias and/or misinterpretation. Thus, in the next chapter I quantify the findings from the identified studies to statistically synthesize and perform meta-analyses that explore the role of the SVC in VSTM according to the systematically identified data from previous TMS studies.

3 Sensory Recruitment in Visual Short-Term Memory: Meta-Analyses of Sensory Visual Cortex Interference Using Transcranial Magnetic Stimulation

A version of this chapter has been published elsewhere (see Phylactou et al., 2022).

3.1 Chapter 3 Introduction

Building on the systematic identification of previous studies that have interfered with TMS on the SVC during VSTM from Chapter 2, here, I discuss the quantitative assessment of these studies.

3.1.1 Objective

My specific aim in Chapter 3 was to quantitively synthesize the findings of those studies identified in the previous Chapter, using meta-analytic methods. Specifically, two meta-analyses were conducted. The aim of the first meta-analysis was to assess the size of the TMS effect during the encoding VSTM phase, whereas the second meta-analysis aimed to explore and quantify the presence of an effect during the maintenance VSTM phase and compare it to the encoding effect. Additionally, heterogeneity between the identified studies and small study bias was explored. Further, because of the variety of the timings that TMS was induced during VSTM in the included studies, I performed two meta-regressions to explore whether TMS timing (1) after stimulus offset and (2) after stimulus onset were correlated to the TMS effect. Even though meta-analytic methodology is more common in clinical research, guidelines have been recently proposed for implementing meta-analyses for basic scientific questions (Mikolajewicz & Komarova, 2019).

3.2 Methods

3.2.1 Study Selection

Out of the 14 articles that were identified through the PRISMA protocol (see Figure 2.1) in Chapter 2, seven provided sufficient statistical data to estimate effect sizes and thus be included in the meta-analyses. The corresponding authors of the remaining papers were contacted through email and further data were requested in order to compute effect sizes and therefore make the studies eligible for the quantitative analysis of this review. One author responded by providing additional data and thus making the final number of included studies in the meta-analyses eight. In order for the studies identified in Chapter 2 to be included in the meta-analyses, they further had to provide arithmetic data (means and SDs or *t* scores) on behavioral performance scores during a VSTM task in a TMS interference condition and at least one control condition. These variables varied according to study design (i.e., different measures for match-to-sample tasks than for change-detection tasks) and included measurements of accuracy, absolute error, percent correct, precision, guess rate and signal detection (*A'*).

3.2.2 Data Analysis

Effect sizes were calculated as the standardized difference between behavioral measures (i.e., accuracies, guess rates, precision, or signal detection) of the experimental condition (i.e., where TMS was induced in the corresponding V1 or V5/MT+ as reported by the authors) and the control condition (i.e., sham TMS, no TMS, weak TMS, or TMS administered to an irrelevant brain area as reported by the authors).

Eight studies provided sufficient statistical data to be included in the meta-analyses. Two meta-analyses were performed: (1) one for experiments inducing TMS during VSTM encoding and (2) one for experiments inducing TMS during VSTM maintenance.

Due to methodological differences between TMS studies (see de Graaf, & Sack, 2011), significant heterogeneity, as indicated with the I^2 index was expected between the studies (van de Ven & Sack, 2013). According to Higgins, Thompson, Deeks, and Altman (2003), the I^2 index levels can be described as low, moderate, and high, when they fall close to 25%, 50%, and 75%, respectively. I estimated effect sizes for each individual data set using Hedge's *g* formula (Hedges, 1981). In order to quantify the overall effect size of TMS, I used the absolute values of the effect sizes in my meta-analysis models (see Fritz et al.,2012; Morrissey, 2016), which has several advantages compared to the use of signed effect sizes. Specifically, absolute effect sizes avoid alternative explanations for the inhibitory and facilitatory TMS effects that were identified and cannot be explored due to the small number of the included studies that restrict me from exploring moderator effects in the analyses. Further, because the effect sizes were calculated from different types of behavioral measures, using the signed effect sizes would require reversing the signs of some effect sizes so that they all point towards enhancement or inhibition. For example, an effect size greater than 0 calculated from guess rates indicates a performance drop, while a similar effect size calculated from percent correct shows performance increase. Moreover, using the signed effect sizes may lead to bias in the conclusions. As an example, in studies that compare VSTM performance in contralateral versus ipsilateral sensory visual cortex TMS it is unclear if a difference in performance reflects TMS inhibition or facilitation. For example, a study that treated TMS over the contralateral sensory visual cortex as the experimental condition and TMS over the ipsilateral side as the control condition will interpret a performance drop (e.g., contralateral accuracy < ipsilateral accuracy) as an inhibitory TMS effect. However, given recent evidence supporting the role of the ipsilateral sensory visual cortex in visual processing (Zhao et al., 2021) and the visual pathway neuroanatomy (see Joukal, 2017; Wichmann & Müller-Forell, 2004), it could be reasonable to assume that the ipsilateral sensory visual cortex is in fact the experimental condition. In such a case, the conclusion of the same study, with a different definition of the experimental and control conditions might turn out to be the opposite (e.g., facilitation effects since ipsilateral accuracy > contralateral accuracy). I therefore opted to use the absolute values of the effect sizes which were then pooled using a random-effects model (Fleiss, 1993).

Data analysis was conducted using R (v4.0.2) and Rstudio (v1.1.456) (R Core Team, 2020; see also Harrer et al., 2019). Hedge's *g* (Hedges, 1981) effect sizes were calculated using the esc library (Lüdecke, 2018). The effect sizes were pooled using a random effects model (Fleiss, 1993) using the meta package for R (Schwarzer, 2007). Specifically, the meta-analyses were conducted using the inverse variance method, where variance includes both within- and between-study variance. The maximum-likelihood estimator was used for tau^2 and the Q-profile method was used for the *tau* and tau^2 confidence intervals. Forest plots were used for data visualization. Due to the small number of studies included in the meta-analyses, moderator variables analysis was not possible to conduct. To test for small study bias, funnel plots were generated to visually investigate their symmetry which was further examined using the Egger's test

(Egger et al., 1997). Mikolajewicz and Komarova (2019) provide a comprehensive summary for how Hedge's *g*, tau^2, *Q*, and I^2 are formulated.

Some individuals participated in more than one experiment and/or experimental condition. Because this violates the independency of some data points, I performed a three-level meta-analysis (see Assink & Wibbelink, 2016; Cheung, 2014; Pastor & Lazowski, 2018). I included an additional level in the meta-analyses, referred here as the study level, where I clustered each experiment and/or experimental condition to its corresponding study. This analysis allowed me to explore how the different levels explain variance in the model. I then repeated the analyses excluding the study level and compared the fitness of the two-level and three-level models.

Lastly, since the timing of the induced TMS varied between the included studies, I performed two meta-regressions on the calculated effect sizes using the TMS timing point of each effect size as a covariate; one for TMS timing after stimulus offset, and one for TMS timing after stimulus onset. These meta-regressions served a double purpose: (1) explore whether stimulation timing can predict the TMS effect and (2) explore whether the TMS effect differs according to the stimulation timing without categorizing it in one of the two VSTM phases.

All relevant data used in this Chapter are openly available and can be accessed on https://osf.io/p8nwz.

3.3 Results

3.3.1 Meta-analysis 1: Transcranial Magnetic Stimulation Interference During Encoding

Five studies totalling *n* = 204 participants were included in the meta-analysis investigating the effect of TMS during the encoding of visual information. Out of these five studies, a total of 18 effect sizes were calculated based on all the relevant experimental conditions. All effect sizes are presented in Table 3.1.

Table 3. 1: Experiments included in the meta-analysis of sensory visual cortex transcranial magnetic stimulation during the encoding phase of a visual short-term memory task.

	Study	**Effect Size**	**Standard Error**	**Z**	**p**	**N**	**Behavioral Measure (Condition)**	**Control Condition**
1	Cattaneo et al (2009)a	0.82	0.32	2.55	0.01	14	Accuracy	No TMS
2	Cattaneo et al (2009)b	0.64	0.30	2.11	0.03	14	Accuracy	Sham TMS
3	van de Ven et al (2012)a	0.36	0.31	1.16	0.25	12	Detection Sensitivity *A'* (LL)	Ipsilateral SVC
4	van de Ven et al (2012)b	0.23	0.31	0.75	0.46	12	Detection Sensitivity *A'* (HL)	Ipsilateral SVC
5	van de Ven et al (2012)c	0.00	0.31	0.00	1.00	12	Detection Sensitivity *A'* (LL)	Ipsilateral SVC
6	van de Ven et al (2012)d	0.97	0.34	2.82	<0.01	12	Detection Sensitivity *A'* (HL)	Ipsilateral SVC
7	Koivisto et al (2017)a	3.45	0.65	5.35	<0.01	12	Proportion of Guess (Exp1 60 ms)	No TMS
8	Koivisto et al (2017)b	3.81	0.69	5.49	<0.01	12	Proportion of Guess (Exp1 90 ms)	No TMS
9	Koivisto et al (2017)c	3.15	0.60	5.28	<0.01	12	Proportion of Guess (Exp1 120 ms)	No TMS
10	Koivisto et al (2017)d	0.42	0.43	0.97	0.33	7	Proportion of Guess (Exp2 120 ms)	Ipsilateral SVC
11	Koivisto et al (2017)e	0.64	0.45	1.43	0.15	7	Proportion of Guess (Exp2 150 ms)	Ipsilateral SVC
12	Koivisto et al (2017)f	0.09	0.42	0.21	0.83	7	Proportion of Guess (Exp3 150 ms)	Ipsilateral SVC
13	Koivisto et al (2017)g	0.22	0.42	0.52	0.60	7	Proportion of Guess (Exp2 120 ms)	No TMS
14	Koivisto et al (2017)h	0.50	0.44	1.15	0.25	7	Proportion of Guess (Exp2 150 ms)	No TMS
15	Koivisto et al (2017)i	0.06	0.42	0.14	0.89	7	Proportion of Guess (Exp3 150 ms)	No TMS
16	Rademaker et al (2017)	0.32	0.39	0.81	0.42	8	Absolute Error	Sham TMS
17	van Lamsweerde et al (2017)a	0.11	0.22	0.49	0.62	21	Guess Rate (100 ms)	Ipsilateral SVC

Notes. HL; high load condition, LL; low load condition, SVC; sensory visual cortex, TMS; transcranial magnetic stimulation, VSTM; visual short-term memory.

As expected, heterogeneity was significant amongst data sets, $Q(17) = 75.67$, $p < .0001$, with high inconsistency between studies, $I^2 = 77.5\%$, $\tau^2 = .80$, 95% $CI = .47, 2.94$. I proceeded with a random effects model which provided a significant standardized difference in means of *g* = .80, 95% *CI* = .35, 1.25, *Z* = 3.46, *p* = .0005, indicating that TMS during encoding on the sensory visual cortex does have a high effect on VSTM behavioral outcomes. The forest plot of the meta-analysis during encoding is illustrated in Figure 3.1 (top).

Figure 3. 1: Meta-analyses of sensory visual cortex transcranial magnetic stimulation on visual short-term memory performance.

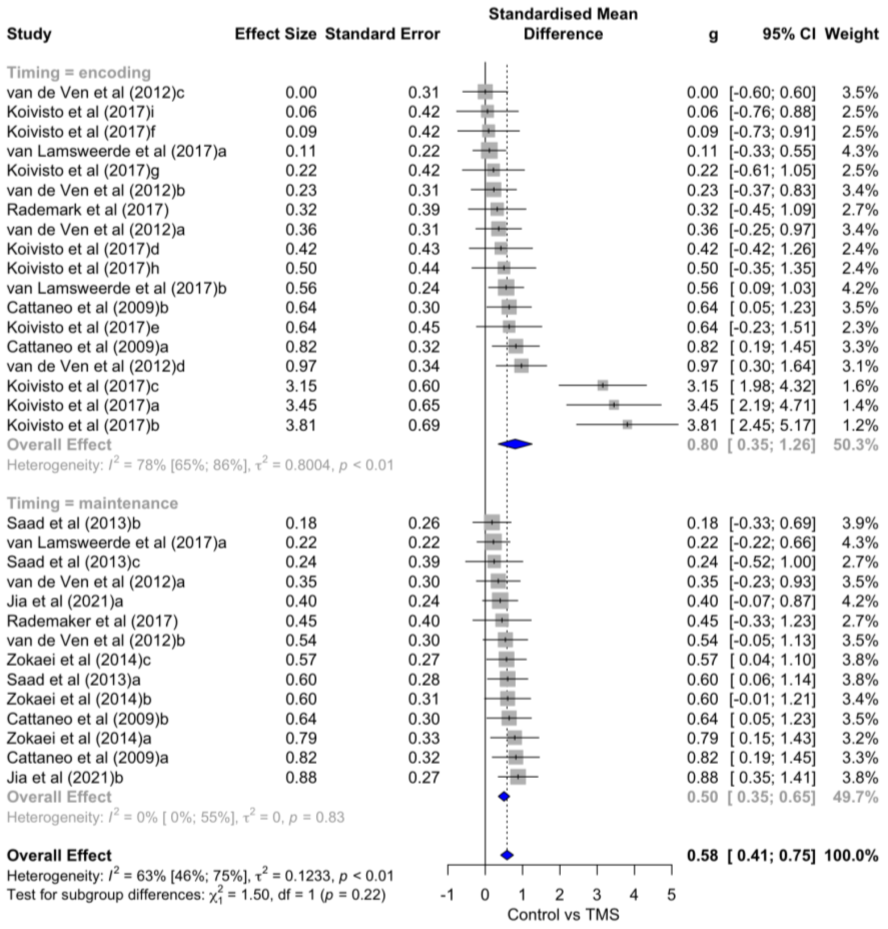


Fig.3.1. The meta-analyses of behavioral outcomes when inducing TMS on the SVC during a VSTM task. The forest plot of a random effects model pooling the effect sizes of experiments inducing TMS on SVC during the encoding phase (top) and maintenance phase (bottom) of a VSTM task. In both meta-analyses the overall standard means difference indicates that TMS does have an effect on behavior when induced on the SVC, and these two overall effects do not differ between them. An overall effect including all studies (both encoding and maintenance) show a significantly high effect of TMS. SVC; sensory visual cortex, TMS; transcranial magnetic stimulation, VSTM; visual short-term memory.

Further, small study bias was investigated using visual inspection of a generated funnel plot (see Figure 3.2A) and using the Egger's Test. The right side of the inverted funnel is underrepresented, indicating that more studies showing a stronger TMS interference effect in VSTM encoding are needed to make the funnel symmetrical. Both approaches indicated possible small study bias, as reflected in the asymmetry of the funnel plot and the significant Egger's Test, *intercept* = 4.85, *t*(17) = 3.59, *p* = .002.

Figure 3. 2: Funnel plots of studies included in the sensory visual cortex transcranial magnetic stimulation meta-analyses.

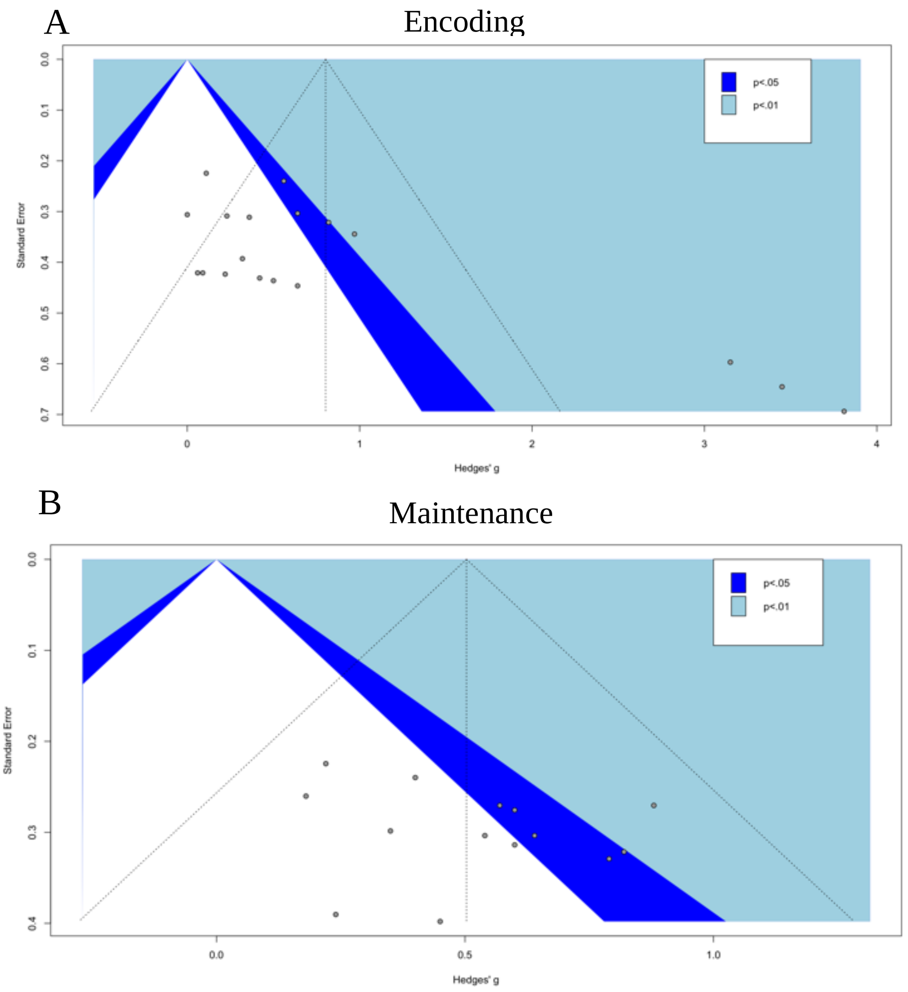


Fig.3.2. The funnel plots of the identified experiments in (**A**) encoding and (**B**) maintenance to investigate publication bias show an asymmetry between the data points, indicating publication bias.

3.3.2 Meta-analysis 2: Transcranial Magnetic Stimulation Interference During Maintenance

A total of seven studies totaling *n* = 206 participants were included in the meta-analysis of the effect of TMS during the maintenance of visual information. From the relevant experimental conditions of these seven studies, a total of 14 effect sizes were calculated. The effect sizes are presented in Table 3.2.

Table 3. 2: Experiments included in the meta-analysis of sensory visual cortex transcranial magnetic stimulation during the maintenance phase of a visual short-term memory task.

	Study	**Effect Size**	**Standard Error**	**Z**	**p**	**N**	**Behavioral Measure (Condition)**	**Control Condition**
1	Cattaneo et al (2009)a	0.82	0.32	2.55	0.01	14	Accuracy	No TMS
2	Cattaneo et al (2009)b	0.64	0.30	2.11	0.04	14	Accuracy	Sham TMS
3	van de Ven et al (2012)a	0.35	0.30	1.17	0.24	12	Detection Sensitivity *A'* (LL)	Ipsilateral SVC
4	van de Ven et al (2012)b	0.54	0.30	1.78	0.08	12	Detection Sensitivity *A'* (HL)	Ipsilateral SVC
5	Saad et al (2013)a	0.60	0.28	2.18	0.03	16	Accuracy (Exp2 2000 ms)	Sham TMS
6	Saad et al (2013)b	0.18	0.26	0.69	0.49	16	Accuracy (Exp2 5000 ms)	Sham TMS
7	Saad et al (2013)c	0.24	0.39	0.61	0.54	8	Accuracy (Exp3 5000 ms)	Sham TMS
8	Zokaei et al (2014)a	0.79	0.33	2.40	0.02	13	Precision (Exp 1 congruent)	Sham TMS
9	Zokaei et al (2014)b	0.6	0.31	1.91	0.06	13	Precision (Exp 1 incongruent)	Sham TMS
10	Zokaei et al (2014)c	0.57	0.27	2.11	0.04	17	Precision (Exp 2 Item 1)	Sham TMS
11	Rademaker et al (2017)	0.45	0.40	1.13	0.26	8	Absolute Error	Sham TMS
12	van Lamsweerde et al (2017)a	0.22	0.22	0.98	0.33	21	Guess Rate (200ms)	Ipsilateral SVC
13	Jia et al. (2021)a	0.4	0.24	1.13	0.26	20	Accuracy (pre-training)	Sham TMS
14	Jia et al. (2021)b	0.88	0.27	3.25	<0.01	20	Accuracy (post-training)	Sham TMS

Notes. HL; high load condition, LL; low load condition SVC; sensory visual cortex, TMS; transcranial magnetic stimulation, VSTM; visual short-term memory

Heterogeneity was not violated amongst the data sets, $Q(13) = 8.23$, $p = .83$, with no inconsistency between studies, $I^2 = 0\%$, $\tau^2 = 0$, 95% $CI =$ 0, .05. Given the methodological differences used in the included studies, this was an unexpected finding. However, it must be noted that the I^2 confidence intervals were wide ($CI = 0\%, 55\%$), thus making any conclusions regarding heterogeneity difficult to reach. The random effects model provided a significant standardized difference in means of $g = .50$, 95% $CI = .35, .65$, $Z = 6.51$, $p < .0001$, providing evidence that TMS applied on the sensory visual cortex during the maintenance phase of a VSTM task results in a significant moderate difference on VSTM behavioral outcomes. The forest plot of the second meta-analysis is shown in Figure 3.1 (bottom).

As previously, small study bias was investigated by visually inspecting a generated funnel plot (see Figure 3.2B) and with the Egger's Test. No asymmetry was found in the funnel plot, indicating that effect sizes were evenly distributed, as also confirmed by the Egger's Test, $intercept = 1.50$, $t(13) = 3.92$, $p = .30$. Notably, no values seem to be plotted on the top of the horizontal (y) axis of the funnel plot, which represents lower effect size standard error. This likely reflects the lack of studies with large sample sizes, which have greater statistical power and consequently reduce error. However, the lack of asymmetry evidence is possibly explained by the fact that the effect sizes lay between a narrow range of standard error (0.22 to 0.40).

3.3.3 Comparison of the Two Meta-Analyses

In order to compare the two overall effect sizes, the data from both meta-analyses were analyzed together and an overall random effect was pooled for all 32 effect sizes (see Figure 3.1). The overall test of heterogeneity was significant $Q(31) = 84.03$, $p < .0001$, showing an inconsistency between studies, $I^2 = 63.1\%$, $\tau^2 = 0.12$, 95% $CI = .20, 1.56$. The random effects model of all studies indicated a significant moderate effect of TMS on VSTM performance, $g = .58$, 95% $CI = .41, .75$, $Z = 6.74$, $p < .0001$. Further, a comparison between the encoding and maintenance random effects models, showed no significant differences between the two overall effects, $\chi^2(1) = 1.50$, $p = 0.22$, providing an indication that a sensory visual cortex TMS effect on VSTM performance is similarly evident in both the encoding and maintenance VSTM phases.

The three-level meta-analysis indicated that no variance was explained by the study level, $\sigma^2 = 0$, total $I^2 = 7.45\%$ (see Figure 3.3). An analysis of variance comparison of the two-level model ($df = 2$, $AIC = 73.77$, $BIC = 76.64$) and the three-level model ($df = 3$, $AIC = 75.77$, $BIC = 80.07$) showed no significant differences between them ($p = 1$). Since no variance was explained by the study level, and no significant difference was found between the two-level and three-level models it is not likely that the meta-analysis results were affected by dependent effect sizes' correlations.

Due to the difference in TMS timings of the included studies, I performed two meta-regressions to test whether the stimulation timing could predict the effect size. The first meta-regression was conducted using the TMS timing after stimulus offset for each study as a predictor variable, and indicated that TMS timing after stimulus offset does not predict the effect size, *QM*(1) = 0.58, *p* = 0.45, indicating that TMS effects were likely similar between the included studies, irrelevant of when TMS was induced (Figure 3.4A). Further, since stimulus presentation differed between the included studies, I have performed a second meta-regression using TMS timing after stimulus onset as a predictor variable. Similarly, TMS timing after stimulus onset failed to predict the effect size *QM*(1) = 0.49, *p* = 0.49, indicating a similar TMS effect across the different TMS timing conditions (Figure 3.4B). A comparison of the two meta-regressions provided evidence for a very strong correlation (ρ = .98, *p* < .001), thus

Figure 3. 3: The three-level meta-analyses models.

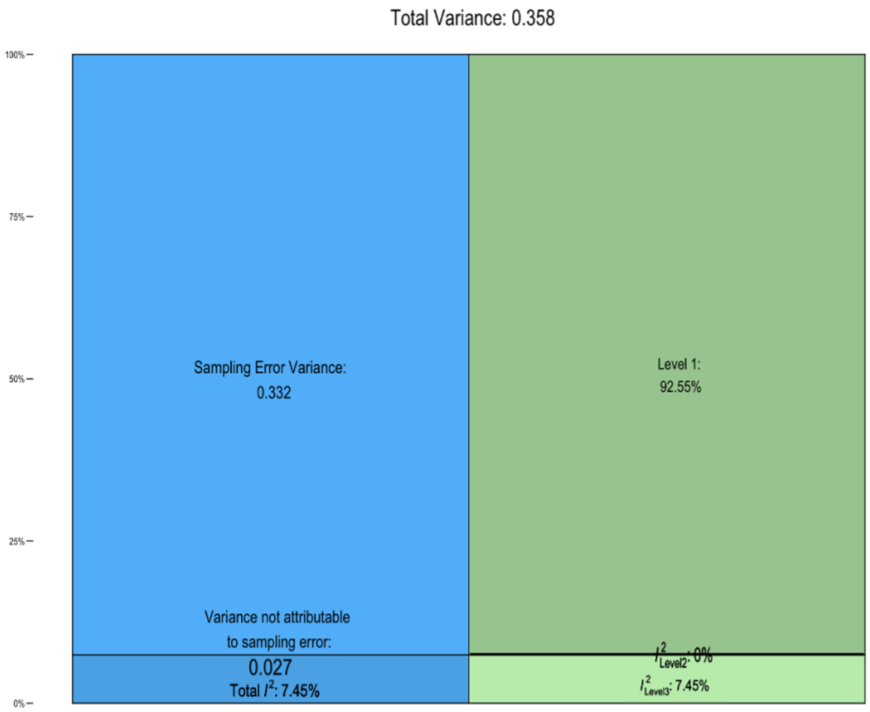
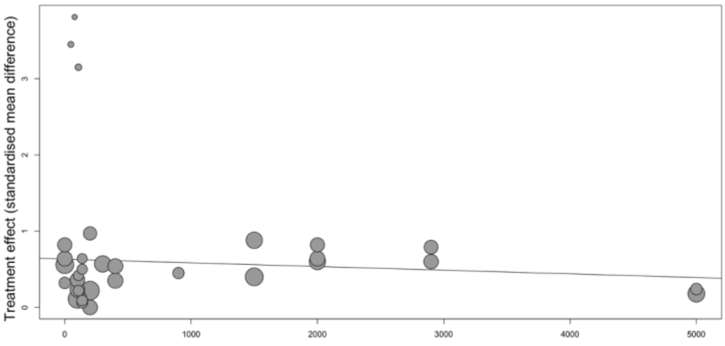


Fig.3.3. The distribution of variance in the three-model meta-analysis, where experiments were clustered to their corresponding studies to introduce the study level (level 2) in the meta-analyses. No variance was explained by level 2 in the three-level models. VSTM; visual short-term memory.

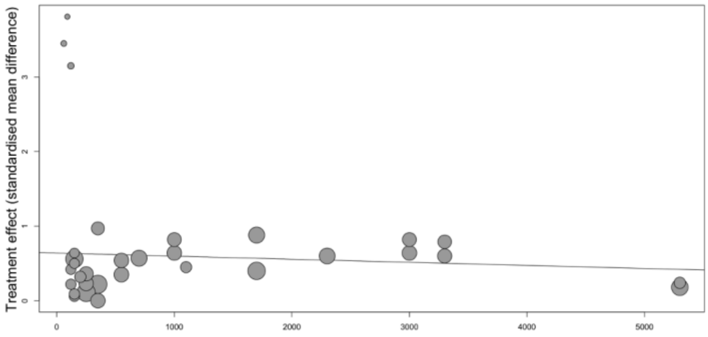
further supporting that the TMS effect is independent from the timing that TMS was induced (Figure 3.4C).

Figure 3. 4: Meta-regression of SVC TMS on VSTM performance predicted by TMS timing.

A Covariate TMS after stimulus offset



B Covariate TMS after stimulus onset



C

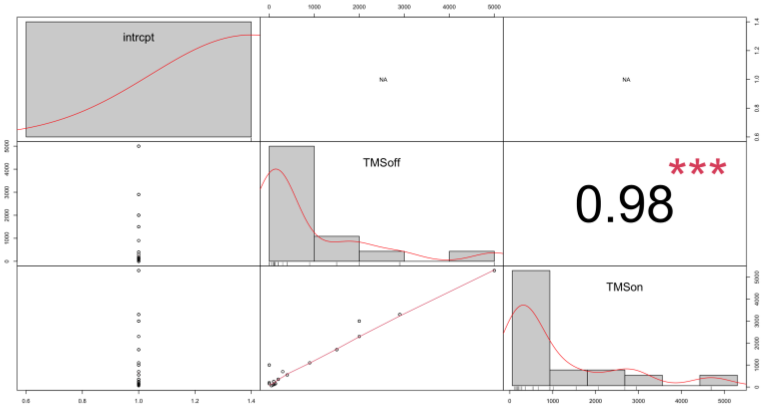


Fig.3.4. The bubble plot of meta-regressions of behavioral outcomes when inducing SVC TMS during a VSTM task, with the different TMS timing points after (A) stimulus offset and (b) stimulus onset used as a predictor variable. The TMS timings fail to predict the studies' effect sizes, as also confirmed by the (C) correlation analysis between the two meta-regressions, indicating that the TMS effects are likely similar independent of the time during the VSTM task that stimulation is induced. SVC; sensory visual cortex, TMS; transcranial magnetic stimulation, VSTM; visual short-term memory.

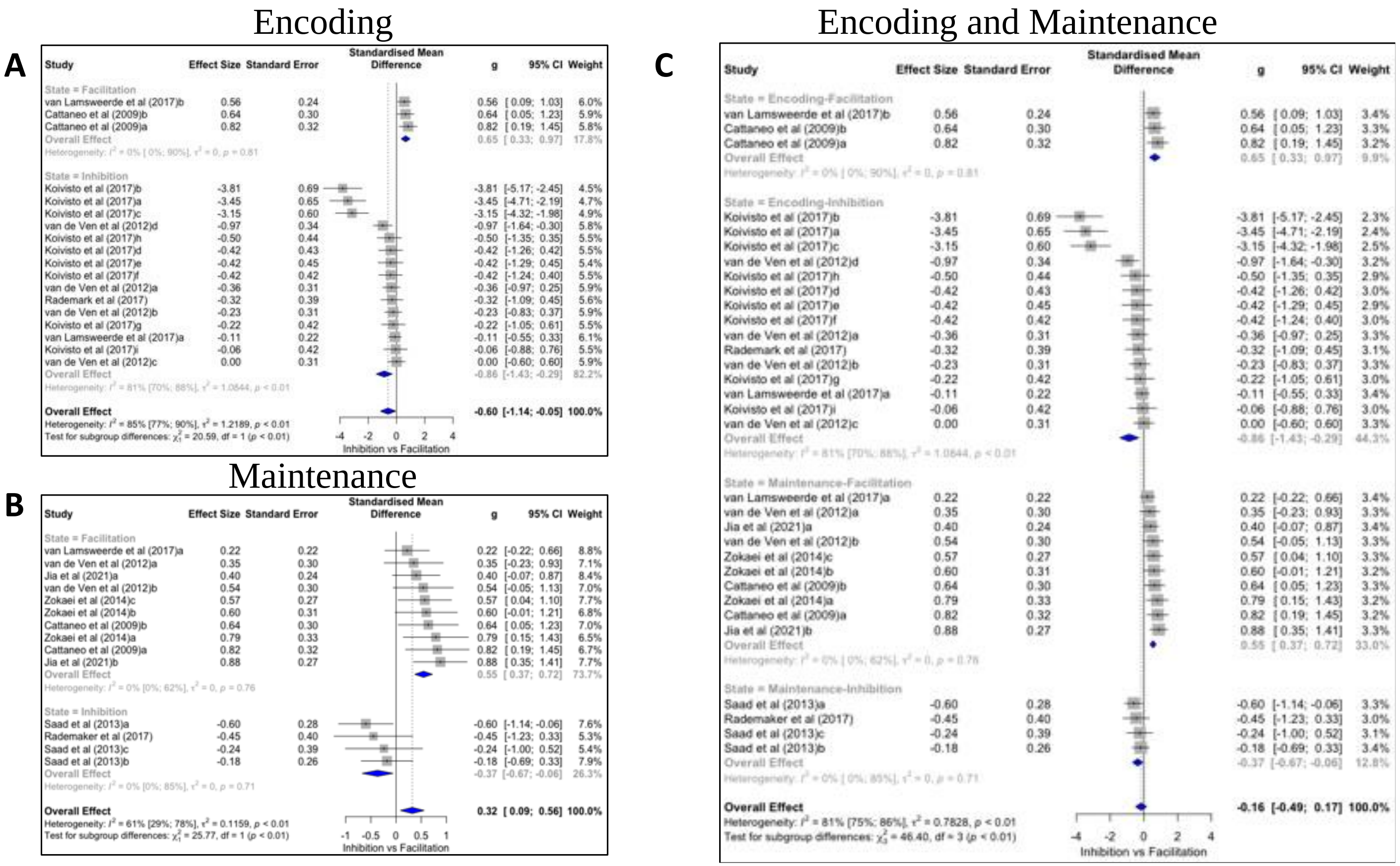
3.3.4 Facilitation versus Inhibition

A third, exploratory, meta-analysis was conducted to explore whether there is evidence in favor of facilitatory or inhibitory TMS effects on VSTM performance. This meta-analysis was conducted on the signed effect sizes. Prior to the analysis the signs of effect sizes from studies measuring guess rates (van Lamsweerde et al., 2017), proportion of guesses (Koivisto et al., 2017), and absolute errors (Rademaker et al., 2017) were reversed, in order to indicate the same direction of effect as those measuring percent correct and detection sensitivity (*A*'). As such, positive values indicate facilitatory TMS effects on VSTM performance, while negative values represent inhibitory TMS effects.

For visualization purposes, studies were categorized into four groups (Figure 3.5), according to TMS timing (encoding or maintenance) and to the direction of the effect (inhibition or facilitation). Regarding encoding (Figure 3.5A), the random effects model provided evidence in favor of a moderate inhibition effect with an overall effect of g = -.60, *95% CI* = -1.14, -.05, Z = -2.15, p = .031. Contrary, there was evidence in favor of a small facilitation effect for maintenance (Figure 3.5B), g = .32, *95% CI* = .09, .56, Z = 2.67, p = .007. Lastly, by considering all 32 effect sizes, there was no indication of a directional effect for sensory visual cortex TMS on VSTM performance (Figure 3.5C), since the overall random effects model failed to reach significance, g = -.16, *95% CI* = -.49, .17, Z = -.95, p = .342.

Overall, the exploratory meta-analysis indicates that the direction of TMS effects on VSTM performance differs between encoding and maintenance. In line with the well-studied role of the sensory visual cortex during VSTM encoding (e.g., Awh & Jonides, 2001; D'Esposito & Postle, 2015; de Graaf et al., 2014; Kammer, 2007; Masse et al., 2020; Serences, 2016; Shevlin, 2020), an inhibition effect (VSTM performance decrease) was evident when TMS was applied during the encoding VSTM phase. In contrast, a facilitation effect (VSTM performance increase) has been found for studies applying TMS during the maintenance VSTM phase. However, TMS effects have been shown to be complex, both on the physiological and on the behavioral outcomes, and often depend on the specific stimulation parameters used, such as intensity, duration, and frequency (Aydin -Abidin et al., 2006; Eldaeif et al., 2011; Kammer et al., 2005; Moliadze et al., 2003). Further, as discussed above (see *3.2.2 Data Analysis*), in some

Figure 3. 5: Exploratory meta-analysis on the direction of SVC TMS on VSTM performance.



Encoding

Study	Effect Size	Standard Error	g	95% CI	Weight
State = Facilitation					
van Lamsweerde et al (2017)b	0.56	0.24	0.56	[0.09; 1.03]	6.0%
Cattaneo et al (2009)b	0.64	0.30	0.64	[0.05; 1.23]	5.9%
Cattaneo et al (2009)a	0.82	0.32	0.82	[0.19; 1.45]	5.8%
Overall Effect			0.65	[0.33; 0.97]	17.8%
Heterogeneity: $I^2 = 0\%$ [0%; 90%], $\tau^2 = 0$, $p = 0.81$					
State = Inhibition					
Koivisto et al (2017)b	-3.81	0.69	-3.81	[-5.17; -2.45]	4.5%
Koivisto et al (2017)a	-3.45	0.65	-3.45	[-4.71; -2.19]	4.7%
Koivisto et al (2017)c	-3.15	0.60	-3.15	[-4.32; -1.98]	4.9%
van de Ven et al (2012)d	-0.97	0.34	-0.97	[-1.64; -0.30]	5.8%
Koivisto et al (2017)h	-0.50	0.44	-0.50	[-1.35; 0.35]	5.5%
Koivisto et al (2017)d	-0.42	0.43	-0.42	[-1.26; 0.42]	5.5%
Koivisto et al (2017)e	-0.42	0.45	-0.42	[-1.29; 0.45]	5.4%
Koivisto et al (2017)f	-0.42	0.42	-0.42	[-1.24; 0.40]	5.5%
van de Ven et al (2012)a	-0.36	0.31	-0.36	[-0.97; 0.25]	5.9%
Rademark et al (2017)	-0.32	0.39	-0.32	[-1.09; 0.45]	5.6%
van de Ven et al (2012)b	-0.23	0.31	-0.23	[-0.83; 0.37]	5.9%
Koivisto et al (2017)g	-0.22	0.42	-0.22	[-1.05; 0.61]	5.5%
van Lamsweerde et al (2017)a	-0.11	0.22	-0.11	[-0.55; 0.33]	6.1%
Koivisto et al (2017)i	-0.06	0.42	-0.06	[-0.88; 0.76]	5.5%
van de Ven et al (2012)c	0.00	0.31	0.00	[-0.60; 0.60]	5.9%
Overall Effect			-0.86	[-1.43; -0.29]	82.2%
Heterogeneity: $I^2 = 81\%$ [70%; 88%], $\tau^2 = 1.0844$, $p < 0.01$					
Overall Effect			**-0.60**	**[-1.14; -0.05]**	**100.0%**
Heterogeneity: $I^2 = 85\%$ [77%; 90%], $\tau^2 = 1.2189$, $p < 0.01$					
Test for subgroup differences: $\chi^2_1 = 20.59$, df = 1 ($p < 0.01$)					

Maintenance

Study	Effect Size	Standard Error	g	95% CI	Weight
State = Facilitation					
van Lamsweerde et al (2017)a	0.22	0.22	0.22	[-0.22; 0.66]	8.8%
van de Ven et al (2012)a	0.35	0.30	0.35	[-0.23; 0.93]	7.1%
Jia et al (2021)a	0.40	0.24	0.40	[-0.07; 0.87]	8.4%
van de Ven et al (2012)b	0.54	0.30	0.54	[-0.05; 1.13]	7.0%
Zokaei et al (2014)c	0.57	0.27	0.57	[0.04; 1.10]	7.7%
Zokaei et al (2014)b	0.60	0.31	0.60	[-0.01; 1.21]	6.8%
Cattaneo et al (2009)b	0.64	0.30	0.64	[0.05; 1.23]	7.0%
Zokaei et al (2014)a	0.79	0.33	0.79	[0.15; 1.43]	6.5%
Cattaneo et al (2009)a	0.82	0.32	0.82	[0.19; 1.45]	6.7%
Jia et al (2021)b	0.88	0.27	0.88	[0.35; 1.41]	7.7%
Overall Effect			0.55	[0.37; 0.72]	73.7%
Heterogeneity: $I^2 = 0\%$ [0%; 62%], $\tau^2 = 0$, $p = 0.76$					
State = Inhibition					
Saad et al (2013)a	-0.60	0.28	-0.60	[-1.14; -0.06]	7.6%
Rademaker et al (2017)	-0.45	0.40	-0.45	[-1.23; 0.33]	5.3%
Saad et al (2013)c	-0.24	0.39	-0.24	[-1.00; 0.52]	5.4%
Saad et al (2013)b	-0.18	0.26	-0.18	[-0.69; 0.33]	7.9%
Overall Effect			-0.37	[-0.67; -0.06]	26.3%
Heterogeneity: $I^2 = 0\%$ [0%; 85%], $\tau^2 = 0$, $p = 0.71$					
Overall Effect			**0.32**	**[0.09; 0.56]**	**100.0%**
Heterogeneity: $I^2 = 61\%$ [29%; 78%], $\tau^2 = 0.1159$, $p < 0.01$					
Test for subgroup differences: $\chi^2_1 = 25.77$, df = 1 ($p < 0.01$)					

Encoding and Maintenance

Study	Effect Size	Standard Error	g	95% CI	Weight
State = Encoding-Facilitation					
van Lamsweerde et al (2017)b	0.56	0.24	0.56	[0.09; 1.03]	3.4%
Cattaneo et al (2009)b	0.64	0.30	0.64	[0.05; 1.23]	3.3%
Cattaneo et al (2009)a	0.82	0.32	0.82	[0.19; 1.45]	3.2%
Overall Effect			0.65	[0.33; 0.97]	9.9%
Heterogeneity: $I^2 = 0\%$ [0%; 90%], $\tau^2 = 0$, $p = 0.81$					
State = Encoding-Inhibition					
Koivisto et al (2017)b	-3.81	0.69	-3.81	[-5.17; -2.45]	2.3%
Koivisto et al (2017)a	-3.45	0.65	-3.45	[-4.71; -2.19]	2.4%
Koivisto et al (2017)c	-3.15	0.60	-3.15	[-4.32; -1.98]	2.5%
van de Ven et al (2012)d	-0.97	0.34	-0.97	[-1.64; -0.30]	3.2%
Koivisto et al (2017)h	-0.50	0.44	-0.50	[-1.35; 0.35]	2.9%
Koivisto et al (2017)d	-0.42	0.43	-0.42	[-1.26; 0.42]	3.0%
Koivisto et al (2017)e	-0.42	0.45	-0.42	[-1.29; 0.45]	2.9%
Koivisto et al (2017)f	-0.42	0.42	-0.42	[-1.24; 0.40]	3.0%
van de Ven et al (2012)a	-0.36	0.31	-0.36	[-0.97; 0.25]	3.3%
Rademark et al (2017)	-0.32	0.39	-0.32	[-1.09; 0.45]	3.1%
van de Ven et al (2012)b	-0.23	0.31	-0.23	[-0.83; 0.37]	3.3%
Koivisto et al (2017)g	-0.22	0.42	-0.22	[-1.05; 0.61]	3.0%
van Lamsweerde et al (2017)a	-0.11	0.22	-0.11	[-0.55; 0.33]	3.4%
Koivisto et al (2017)i	-0.06	0.42	-0.06	[-0.88; 0.76]	3.0%
van de Ven et al (2012)c	0.00	0.31	0.00	[-0.60; 0.60]	3.3%
Overall Effect			-0.86	[-1.43; -0.29]	44.3%
Heterogeneity: $I^2 = 81\%$ [70%; 88%], $\tau^2 = 1.0844$, $p < 0.01$					
State = Maintenance-Facilitation					
van Lamsweerde et al (2017)a	0.22	0.22	0.22	[-0.22; 0.66]	3.4%
van de Ven et al (2012)a	0.35	0.30	0.35	[-0.23; 0.93]	3.3%
Jia et al (2021)a	0.40	0.24	0.40	[-0.07; 0.87]	3.4%
van de Ven et al (2012)b	0.54	0.30	0.54	[-0.05; 1.13]	3.3%
Zokaei et al (2014)c	0.57	0.27	0.57	[0.04; 1.10]	3.3%
Zokaei et al (2014)b	0.60	0.31	0.60	[-0.01; 1.21]	3.2%
Cattaneo et al (2009)b	0.64	0.30	0.64	[0.05; 1.23]	3.3%
Zokaei et al (2014)a	0.79	0.33	0.79	[0.15; 1.43]	3.2%
Cattaneo et al (2009)a	0.82	0.32	0.82	[0.19; 1.45]	3.2%
Jia et al (2021)b	0.88	0.27	0.88	[0.35; 1.41]	3.3%
Overall Effect			0.55	[0.37; 0.72]	33.0%
Heterogeneity: $I^2 = 0\%$ [0%; 62%], $\tau^2 = 0$, $p = 0.76$					
State = Maintenance-Inhibition					
Saad et al (2013)a	-0.60	0.28	-0.60	[-1.14; -0.06]	3.3%
Rademaker et al (2017)	-0.45	0.40	-0.45	[-1.23; 0.33]	3.0%
Saad et al (2013)c	-0.24	0.39	-0.24	[-1.00; 0.52]	3.1%
Saad et al (2013)b	-0.18	0.26	-0.18	[-0.69; 0.33]	3.4%
Overall Effect			-0.37	[-0.67; -0.06]	12.8%
Heterogeneity: $I^2 = 0\%$ [0%; 85%], $\tau^2 = 0$, $p = 0.71$					
Overall Effect			**-0.16**	**[-0.49; 0.17]**	**100.0%**
Heterogeneity: $I^2 = 81\%$ [75%; 86%], $\tau^2 = 0.7828$, $p < 0.01$					
Test for subgroup differences: $\chi^2_3 = 46.40$, df = 3 ($p < 0.01$)					

Fig 3.5. Exploring the direction of effects in (**A**) encoding, (**B**) maintenance, and (**C**) all effect sizes. For illustration purposes, effect sizes were categorized as either a facilitation or an inhibition effect. Results are inconclusive, with no evidence of neither facilitation nor inhibition effects of SVC TMS in VSTM behavioral outcomes.

Note: The signs of effect sizes from studies measuring guess rates (van Lamsweerde et al., 2017), proportion of guesses (Koivisto et al., 2017), and absolute errors (Rademaker et al., 2017) were reversed, in order to indicate the same direction of effect as those measuring percent correct and detection sensitivity.
SVC; sensory visual cortex, TMS; transcranial magnetic stimulation, VSTM; visual short-term memory.

cases the interpretation of the TMS effects on behavioral outcomes might be misinterpreted (e.g., when comparing the ipsilateral to the contralateral condition). Therefore, it is possible that different TMS parameters or experimental methods, lead to different behavioral effects. Nevertheless, the exploratory meta-analysis, which can be considered a more conservative approach since it is limited on quantifying the overall effect size of TMS beyond the direction of effects, reflects similar results as the encoding (see *3.3.1 Meta-analysis 1: Transcranial Magnetic Stimulation Interference During Encoding)* and maintenance (see *3.3.2 Meta-analysis 2: Transcranial Magnetic Stimulation Interference During Maintenance*) meta-analyses, by further confirming a stronger TMS effect during VSTM encoding and a weaker TMS effect during VSTM maintenance.

3.4 Chapter 3 Summary

Similarly to the results of the systematic review (see Chapter 2) quantifying the results of the available data using meta-analytic methodology, further supports that the SVC is indeed involved in encoding as well as short-term memory maintenance. This was shown by the evidence favoring the TMS condition over the control condition as indicated by behavioral outcomes of previous studies that were systematically identified. Specifically, eight studies provided sufficient statistical data for meta-analysis and yielded a total of 32 effect sizes, which were included in the meta-analyses. The meta-analyses investigated separately the role of the sensory visual cortex in encoding and short-term maintenance of visual information. The meta-regressions explored whether the different stimulation timings of all included studies are related to the effect of the stimulation. The exploratory meta-analysis investigated the direction of the stimulation effects, indicating an inhibition effect for TMS during VSTM encoding and a facilitatory effect for TMS during VSTM maintenance. The findings indicate that encoding and maintaining visual information in VSTM are both similarly supported by a brain network that includes sensory visual cortex. Moreover, the significant heterogeneity, which was found here, further agrees with the results of the systematic review, by providing additional evidence for the issue of using various methods, parameters, and protocols in TMS research (see *2.3.1 Methodological Issues*). Therefore, in the next chapter I propose a protocol for TMS experimentation, which builds on addressing previous methodological issues, and provides a clear understanding for the causal involvement of the SVC during VSTM maintenance.

4 Causal Evidence for the Role of the Sensory Visual Cortex in Visual Short-Term Memory Maintenance

A version of this chapter has been published elsewhere (see Phylactou, Shimi, & Konstantinou, 2023).

4.1 Chapter 4 Introduction

The systematic review (Chapter 2) and meta-analyses (Chapter 3) indicated that the SVC is similarly involved in both the encoding and maintenance phases of VSTM. The contradicting results of previous TMS studies are likely attributed to the variety of methods applied to study the sensory recruitment framework, as reflected by the significant heterogeneity in the meta-analyses. Moreover, the systematic review identified possible methodological issues with previous studies, which I address in this chapter.

The limitations identified in Chapter 2, reflect probable causes of the mixed results, which have been identified by previous research, and mainly include activity silent mechanisms, feed-forward processes, lack of causal evidence, methodological differences and in some cases methodological oversights (D’Esposito et al., 1999; D’Esposito & Postle, 2015; Masse et al., 2020; Serences, 2016; Xu, 2017, 2020). As covered in section *1.4 Understanding Sensory Recruitment: The Value of Transcranial Magnetic Stimulation*, an ideal hypothetical scenario for investigating whether activity in SVC is required for VSTM maintenance would involve its complete inactivation during the retention interval of a VSTM task and reactivation immediately before the memory probe display (Scimeca et al., 2018; see also Figure 1.11). TMS during the retention interval of a VSTM task can approximate this scenario. Targeted TMS at the SVC has been shown to directly interfere with cortical activity, by using a coil to transfer electromagnetic stimulation at localized brain areas, making the exploration of causal evidence plausible (de Graaf et al., 2014; Pitcher et al., 2020; Tapia et al., 2014; van de Ven & Sack, 2013). Further, TMS has been shown reliable beyond the SVC’s silent activity (Rose et al., 206) and it is thought to be a safe tool for healthy participants, as well as a valuable method for solving neuroscientific research questions (de Graaf & Sack, 2011; Hallet, 2000; Pascual-Leone et al., 2000; Pitcher et al., 2020; Sack, 2006).

As seen in the systematic review (Chapter 2), previous studies have attempted to directly investigate the role of the SVC in VSTM using TMS (Cattaneo et al., 2009; Jia et al., 2021; Rademaker et al., 2017; Silvanto & Cattaneo, 2010; van de Ven & Sack, 2012; van Lamsweerde & Johnson, 2017). To explore this relationship, TMS was combined with delayed change detection or match-to-sample tasks. In these tasks, a memory set is presented to participants in order to be remembered. The memory array is followed by a maintenance delay period, at the end of which individuals are requested to compare (or match) a probe with the remembered information. The SVC is stimulated at different VSTM phases, to make casual inferences based on the temporal point of the TMS interference. In most experiments, stimulation was induced on the SVC of one hemisphere, while stimuli were presented either in the ipsilateral or contralateral (to the stimulation site) visual hemifield in a counterbalanced manner (Cattaneo et al., 2009; Rademaker et al., 2017; van de Ven & Sack, 2012; van Lamsweerde & Johnson, 2017). To draw evidence and reach a conclusion, comparisons between the ipsilateral versus the contralateral conditions (Cattaneo et al., 2009; Rademaker et al., 2017; van de Ven & Sack, 2012; van Lamsweerde & Johnson, 2017), and between real versus sham TMS (Cattaneo et al., 2009; Jia et al., 2021; Rademaker et al., 2017; Silvanto & Cattaneo, 2010) were explored.

As with different methodological approaches, results from previous TMS studies were controversial regarding the sensory recruitment framework. Some of the studies were in support of sensory recruitment (Cattaneo et al, 2019; Jia et al., 2021; Silvanto & Cattaneo, 201) some rejected it (Rademaker et al., 2017; van Lamsweerde & Johnson, 2017) while others were unclear (van de Ven et al., 2012). I suggest that the ambiguous and inconclusive findings of the previous TMS studies, are due to methodological omissions. As reflected by the systematic review in Chapter 2, a careful examination of the methods used in these studies reveals a number of important methodological problems that may have underestimated the contribution of the SVC in VSTM. The most vital issue in the majority of these TMS studies, is that previous researchers considered that when information was presented on one side of the visual hemifield (either right or left side near the center of the monitor), the contralateral SVC processed it. Therefore, stimuli were presented binocularly to the participants either in the left or right visual field, and a contralateral SVC TMS was applied to be compared to an ipsilateral control condition (see section *1.4.1 Transcranial Magnetic Stimulation as a Reliable Tool to Explore Sensory Recruitment*). However, considering the neuroanatomy of the visual pathway system, the binocular presentation of stimuli either left or right close to the center of a screen, and therefore close to the middle of the visual field -as presented in the majority of the previous studies- does not accurately correspond to the contralateral SVC, and could in fact be processed by the ipsilateral one (see Gibaldi et al., 2021; Joukal, 2017; Wichmann & Müller-Forell, 2004). Also, given the neural bases of the visual system, it is possible that information enters the SVC in both brain's hemispheres (Tong et al., 2006), since the visual field of both eyes overlap in certain areas (within 15° of visual angle) of the visual field (Gibaldi et al., 2021; Wichmann & Müller-Forell, 2004). Consequently, it is possible for some TMS effects to be falsely interpreted or remain undetectable (e.g., if information processing happens in both hemispheres despite the contralateral and ipsilateral conditions; de Graaf et al., 2011). For example, as pointed out in Chapter 2, a study that considers the contralateral TMS condition as the experimental condition and the ipsilateral side as the control condition will interpret a performance drop (e.g., contralateral performance < ipsilateral performance) as an inhibitory TMS effect. Nevertheless, considering the evidence supporting the role of the ipsilateral SVC in visual processing (Zhao et al., 2021) and the neuroanatomy of the visual pathway (Wichmann & Müller-Forell, 2004), it is possible that the ipsilateral SVC is in reality the experimental condition. As such, the conclusion of this study, might turn out to be the opposite (e.g., facilitation effects since ipsilateral accuracy > contralateral accuracy), if the experimental and control conditions are inversely defined.

Another important shortcoming of the TMS literature relates to the complexity of the stimuli used in the memory array. In a given memory array, there is a minimal representational requirement for VSTM, based on the core features (e.g., color, orientation, shape) of stimuli. A greater combination of stimuli features increases complexity and VSTM capacity requirements (Alvarez & Cavanagh, 2004). Previous TMS studies used various stimuli in their memory tasks, some of which were complex stimuli such as abstract shapes (van de Ven et al., 2012). However, the evidence leading to the sensory recruitment framework emphasized the selective engagement of the SVC in elemental visual features such as orientation, contrast, and direction of movement (Harrison & Tong, 2009; Issa et al., 2008; Konstantinou et al., 2012; Serences et al., 2009). For example, Jia and colleagues (2021), indeed found a strong TMS effect in a VSTM task requiring participants to remember the elemental visual feature of orientation of one grating. However, in a study requiring participants to remember either one (low load) or three (high load) abstract shapes (that are thought to be complex stimuli consisting of a combination of elemental visual features; van de Ven et al., 2012), TMS did not affect performance in the low load condition of remembering a complex shape (TMS effects were evident only during the high load condition). Such findings suggest that when stimulus complexity increases, higher order brain areas, such as the intraparietal sulcus (Xu & Chun, 2006; Xu, 2007) and the posterior parietal cortex (Song & Jiang, 2006), might be more actively recruited for VSTM. Thus, the neural processes required for successful maintenance of complex visual stimuli in VSTM might be more dependent on higher order brain areas than those required for simple stimuli consisting of elemental visual features, given the high selectivity of SVC in processing of elemental features (Teng & Postle, 2021). This might explain some of the null effects of SVC TMS during the memory delay, since complex representations are likely protected through a more distributed VSTM network (Lorenc & Sreenivasan, 2021; see also Gayet et al., 2018; Scimeca et al., 2018). Hence, it is possible that some of the previous studies failed to find evidence in favor of the SVC involvement in VSTM due to using complex, rather than simple, stimuli.

Therefore, to provide causal evidence for the role of the SVC during VSTM maintenance more robustly, the methodological limitations of previous TMS studies need to be addressed. In particular, the two visual hemifields must be reliably separated so that the visual input is processed by only one occipital hemisphere. One way to reliably separate the SVC hemisphere that processes the information entering the visual field is to present the stimuli monocularly. To achieve monocular stimulus presentation, similar methodological principles as those used in binocular rivalry can be implemented (Carmel et al., 2010). In binocular rivalry, different images overlapping in the visual field are presented separately to each eye. Therefore, by presenting an image corresponding only to one eye (thus avoiding rivalry), stimuli will enter the SVC monocularly (Polonsky et al., 2010). Also, given the V1 neuronal response to specific visual features, the memory array should consist of an elemental visual feature known to selectively correspond to the SVC, such as orientation (Harrison & Tong, 2009; Issa et al., 2008; Jia et al., 2021; Serences et al., 2009; Swisher et al., 2010).

4.1.1 Objective

In short, the objective of the current chapter was to provide causal evidence for the role of the SVC during VSTM maintenance using TMS, while ensuring monocular vision (Figure 4.1). As in the systematic review (Chapter 2) and meta-analyses (Chapter 3), in the current chapter, I have also differentiated between early and late TMS, by considering the outcomes of previous studies (Rademaker et al., 2017; van de Ven et al., 2012; van Lamsweerde et al., 2017), and thus, to test my main question of whether the SVC is involved in VSTM I examined the effects of TMS on behavioral performance separately for stimulation induced at 200 ms and 1000 ms (halfway) into the delay period. In two experiments, stimuli were presented in the center of the visual field, which were viewed monocularly. Therefore, based on the neuroanatomy of the visual pathway (Gibaldi et al., 2021; Joukal, 2017; Tong et al., 2006; Wichmann & Müller-Forell, 2004), it was expected that visual information will initially be processed solely by the ipsilateral (to the eye receiving the information) SVC. As a result, and contrary to past experiments, the contralateral SVC served as the control condition. To explore the main question of whether the SVC is involved in VSTM maintenance, the hypotheses focused on testing differences in detection sensitivity (Stanislaw & Todorov, 1999) for a VSTM task in two experiments. In Experiment 1, detection sensitivity was compared between the ipsilateral and contralateral conditions when stimuli were presented monocularly and TMS was applied (1) during perceptual processing (outcome neutral condition; 0 ms after stimulus onset; H1), (2) during early information maintenance (200 ms after stimulus onset; H2), or (3) during late information maintenance (1000 ms after stimulus onset; H3). More specifically, Experiment 1 enabled me to replicate previous, similar, TMS studies, at two different temporal points during the memory delay period, at an early (200 ms condition) and late (1000 ms) maintenance timepoint. Given the established role of the SVC during perceptual processing (0 ms condition), the outcome neutral condition in Experiment 1 (ipsilateral vs contralateral d’ in 0 ms TMS condition) was employed to evaluate the sufficiency of my methods to successfully manipulate SVC activity with TMS. However, as discussed below, it is likely that a comparison between the ipsilateral and contralateral conditions alone, is inadequate to explore the effects of TMS, for example, due to feedback and/or feedforward processes (Zhao et al., 2021) or due to TMS interference affecting both SVC hemispheres (see *4.2.1.3 Experimental Design*). Therefore, in a second experiment, further to the ipsilateral versus contralateral comparison (H4 and H6), I tested whether VSTM performance differed between a TMS and a sham TMS condition (1) during early information maintenance (200 ms after stimulus onset; H5) and (2) during late information maintenance (1000 ms after stimulus onset; H7).

Figure 4. 1: Methodology for ensuring monocular stimulus presentation during sensory visual cortex transcranial magnetic stimulation.

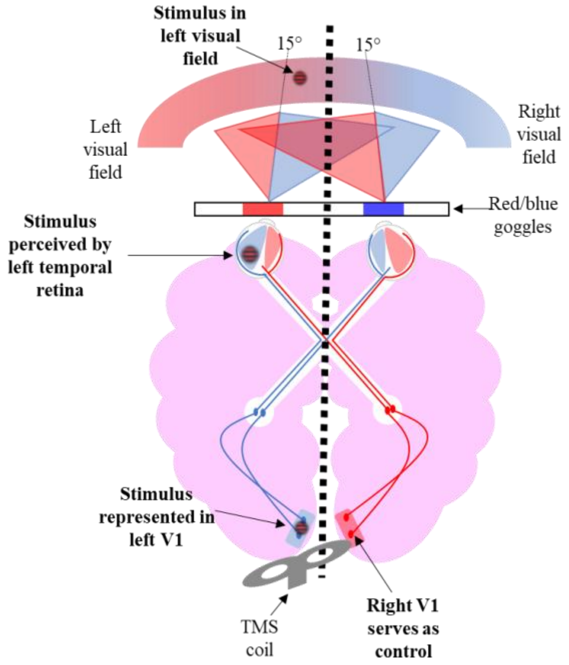


Fig.4.1. When presenting stimuli monocularly and within 15 degrees of visual angle of the left visual field, the stimulus will only enter the left eye's temporal retina and thus be processed by the left V1. Subsequently, the right V1 can serve as a control condition.

4.2 Experiment 1: Transcranial Magnetic Stimulation of the Sensory Visual Cortex During Visual Short-Term Memory

Here I describe a delayed change-detection VSTM task combined with TMS during different temporal points of the memory delay period. In this experiment, I overcome some methodological issues of previous TMS studies (Rademaker et al., 2017; van de Ven et al., 2012; van Lamsweerde et al., 2017). Specifically, to overcome the issue of binocular stimuli presentation and that of the use of complex stimuli, in this TMS experiment I ensure the monocular presentation of stimuli requiring the maintenance of orientation (an elemental visual feature). All experiments presented in this thesis have received ethical approval by the Cyprus National Bioethics Committee (ΕΕΒΚ/ΕΠ/2016/37).

4.2.1 Methods

The hypotheses and methods of this experiment were preregistered and have received in principle acceptance on 06 June 2022 after undergoing peer review from Peer Community in Registered Reports. The accepted Stage 1 protocol can be accessed at https://doi.org/10.17605/OSF.IO/EMPDT.

4.2.1.1 Participants

Sample updating with a stopping rule was set to $BF_{10} > 3$ or $< 1/3$ for all three paired *t*-tests that were performed. However, due to counterbalancing, a minimum of 20 participants (to ensure counterbalancing) or a maximum of 40 participants were to be recruited, given time and resource constraints. Specifically, after data collection for the first 20 participants was completed, I performed my analyses to check if the stopping rule was fulfilled. If any of the three *BFs* did not reach the stopping rule of > 3 or < 1/3, I continued with data collection, as follows: I recruited four additional participants and performed the analyses again. This process was to be repeated until all three *BFs* fulfilled the stopping rule, or until the maximum of 40 participants was reached.

Healthy undergraduate and graduate students from the Cyprus University of Technology were recruited to participate voluntarily. Only individuals with normal or corrected to normal vision were included in the study. Prior to participation, participants were screened for colour deficiencies using the 10-item screening edition Ishihara Colour Deficiency Test, and any individual who showed signs of colour blindness were excluded from the study.

Following the sequential procedure described above, data collection for Experiment 1 was stopped after collecting data from 36 (26 females) participants (Figure 4.2) with mean age 24.25 (*sd* = 4.87) years. In total, 43 participants were recruited for Experiment 1, however, as per my preregistered sampling plan four participants were replaced due to VSTM task performance that was close to chance levels (accuracy < 60%) and three participants were replaced due to vision deficiencies, which were self-reported during study debriefing (amblyopia for two participants, uncorrected astigmatism for one participant). All participants that were replaced were excluded from all analyses.

Figure 4. 2: Sequential and prior robustness analysis for Experiment 1.

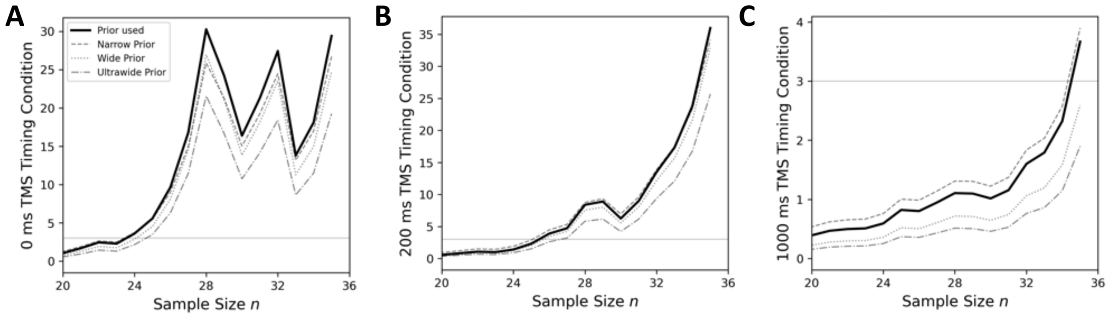


Fig.4.2. Bayes Factor (*BF*) sequential and robustness analysis for the (A) 0 ms, (B) 200 ms, and (C) 1000 ms TMS timing conditions. Following my stopping rule, data collection in Experiment 1 stopped at 36 participants, when the predefined *BF* threshold (*BF* > 3; presented here as the grey horizontal solid line) was reached for all three registered analyses. The *BF* sequential analysis for each registered analysis is shown with a black solid line. The *BF* was informed by a Cauchy distribution centered on 0 with a scaling factor set to (A) *r* = .58, (B) *r* = .8, and (C) *r* = .5. To test the robustness of the *BF*, analyses were repeated for a narrow prior with *r* = .3 (dashed grey line), a wide prior with *r* = 1 (dotted grey line), and an ultrawide prior with *r* = 1.5 (dash-dotted grey line).

Notes. TMS; transcranial magnetic stimulation.

4.2.1.2 Apparatus and Stimuli

A Magstim Super Rapid[2] (MagStim, Whitland, Wales, UK SA34 OHR) stimulator was used for inducing TMS. A Magstim D70 Alpha Flat Coil (Uncoated) delivered a double-pulse TMS at the different experimental conditions. The double-pulse TMS was induced with a frequency of 10 Hz, meaning that stimulation was delivered by two pulses separated by a duration of 100 ms. A 10 Hz double-pulse TMS was chosen to ensure the reliability of the outcome neutral condition. Specifically, the first pulse was induced at the beginning of stimulus presentation and the second pulse at stimulus offset (see *4.2.1.4 Procedure*). Given the possibility that a long encoding time (~100 ms) can lead to successful consolidation despite masking interference (Ye et al., 2017, 2021; Zhang & Luck, 2008), the double-pulse TMS ensured that interference with regular brain activity is introduced throughout the consolidation process (Ye et al., 2017, 2021). For comparison and consistency reasons, the double-pulse TMS was used in all experimental conditions. The stimuli and all experimental procedures were designed and controlled using Python and PsychoPy (Peirce et al., 2019), which were run on an

HP PRODESK desktop computer. To control the TMS, the MagPy TMS package was used (McNair, 2017). Stimuli were presented on a 21.5” Philips 226V^{la} monitor with a 60 Hz refresh rate. A chinrest was placed to ensure that participants maintained a viewing distance of 57 cm from the monitor. Stimuli consisted of either a red (RGB: 255, 0, 0) or a blue (RGB: 0, 0, 255) Gabor patch, which was oriented either horizontally or with a clockwise or counter-clockwise tilt from the horizontal axis, presented on a black (RGB: 0, 0, 0) background (Figure 4.3A). The Gabor patch consisted of a gaussian envelope with a standard deviation of 0.39° (in degrees of visual angle), 0.001° frequency, and had a 1° diameter. Stimuli were presented at fixation. To ensure that the memory array stimulus was viewed monocularly, stimuli were viewed through red/blue anaglyph goggles, consistent with previous research (Haynes et al., 2005), where red stimuli were only viewed by the left eye and blue stimuli only by the right eye (Carmel et al., 2010).

Figure 4. 3: *Stimuli and experimental procedure for investigating the involvement of the sensory visual cortex in visual short-term memory maintenance using transcranial magnetic brain stimulation.*

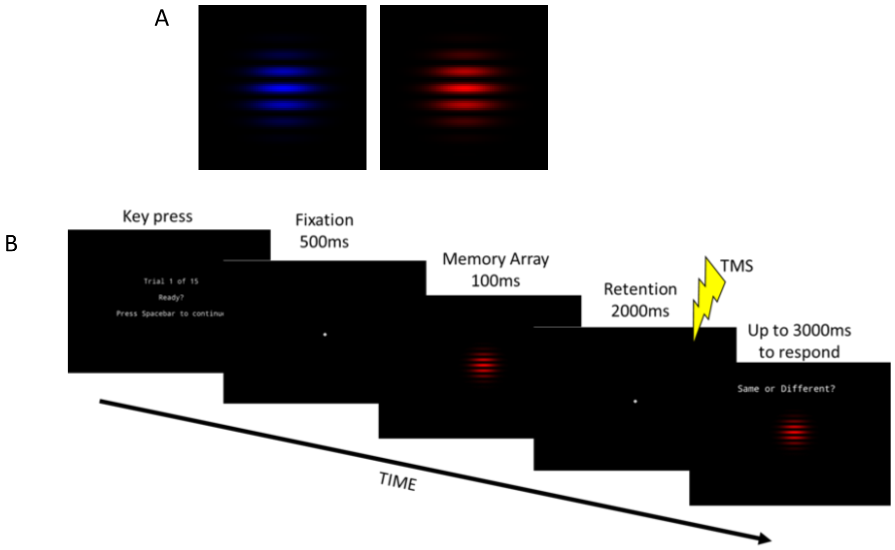


Fig.4.3. (A) Blue and red Gabor patches with a 180° orientation. When viewed through the blue/red anaglygh goggles, blue gratings can only enter the right eye and red ones can only enter the left eye. (B) An example of the delayed change-detection task used in Experiments 1 and 2. The trial begins with a screen indicating the trial number, requesting a keypress to proceed. This is followed by a 500 ms fixation dot. Next, the memory array, consisting of either a red or blue Gabor patch, is shown for 100 ms and participants are asked to memorise its orientation. From the memory array onset, a 2000 ms retention period is presented. During the retention phase, double-pulse TMS is induced at either the left or right sensory visual cortex. In Experiment 1, stimulation is induced at 0 ms, 200 ms, or 1000 ms after the memory array onset. In Experiment 2, either real or sham stimulation is induced at 200 or 1000 ms after the memory array onset. Following the retention period, a probe stimulus is presented at the centre of the screen for up to 3000 ms (or until a response is given), where participants have to respond whether it matches the remembered stimulus or not.

4.2.1.3 Experimental Design

A delayed change-detection VSTM task was conducted where participants were asked to compare the orientation of a probe to the orientation of a remembered grating (memory array) after a 2 second delay period (Figure 4.3B). In half the trials, the probe had the same orientation as the memory array. In the other half, the probe was oriented clockwise (25% of the trials) or counter-clockwise (25% of the trials) to the remembered grating. The experimental procedure is summarized in Figure 4.3B.

Experiment 1 was designed to allow for within-subject comparisons between the ipsilateral and contralateral stimulation conditions at three different TMS timing conditions. Timing conditions refer to the temporal distance of the stimulation after the memory grating's onset. The 0 ms timing condition worked as an outcome neutral test measurement to confirm that my method was reliable to detect TMS effects. Specifically, the first TMS pulse was induced at the onset of the stimulus (at 0 ms) and the second TMS pulse at the offset of the stimulus (at 100 ms, given that the two TMS pulses are separated by a duration of 100 ms). Thus, given the established role of the SVC during visual perception (D'Esposito & Postle, 2015; de Graaf et al., 2014; Kamme, 2007; Serences, 2016, Xu, 2017), evidence for a difference in VSTM performance was expected in the ipsilateral compared to the contralateral condition in the 0 ms condition. The second, 200 ms, condition (first TMS pulse at 200 ms after stimulus onset and second TMS pulse at 300 ms after stimulus onset) shed light on the role of the SVC during the early maintenance phase of VSTM, while the third, 1000 ms, condition (first TMS pulse at 1000 ms after stimulus onset and second TMS pulse at 1100 ms after stimulus onset) allowed the exploration of its role during the later maintenance period. These conditions lead to a two (ipsilateral/contralateral) by three (0 ms/200 ms/1000 ms) design. A total of 432 trials (144 trials per timing condition; 72 with ipsilateral TMS and 72 with contralateral TMS in each timing condition) were gathered, which were divided into six blocks of 72 trials each and presented in a counterbalanced manner across participants.

4.2.1.4 Procedure

Before the main experiment, I localized the right or left SVC of each participant (Cattaneo et al., 2009; Silvanto & Cattaneo, 2010; van de Ven et al, 2012) using the functional method of eliciting phosphenes (Walsh & Pascual-Leone, 2003) and the localization was counterbalanced across participants. Specifically, a tight cap was placed on each participant's head and the inion was marked. Participants were blindfolded but instructed to keep their eyes open using a hollow blindfold. The coil was placed two centimetres above the inion and one centimetre laterally (either left or right based on the participant's group). Starting at a 60% TMS output power, a single-pulse TMS was delivered and participants orally reported whether they have seen phosphenes or not (by saying out loud "yes" or "no"). If no phosphenes are reported after three consecutive stimulations, the procedure was repeated by moving the coil in a one-by-one centimetre grid around the initial stimulation point by approximately 0.2 centimetres, inducing three single-pulse TMS at each position. If a participant still failed to report phosphenes, the same procedure was repeated with a 5% increase on the stimulator output until phosphenes were reported, or until an 80% power on the stimulator was reached. If participants failed to report phosphenes, the localization procedure was repeated on the opposite cortex and if they still failed to perceive phosphenes (see *1.4.2 Transcranial Magnetic Stimulation of the Sensory Visual Cortex*), a fixed output set at 65% of the stimulator's maximum output was used, as has been done previously (Cattaneo et al., 2009; Koivisto et al., 2017; Saad et al., 2015). When the participants successfully reported phosphenes, a mark was placed on the cap and a mechanical arm stabilized the TMS coil and together with the chinrest, this held the participant's head stable on that point. The TMS coil was stabilized at the position where participants reported phosphenes as close to the center of the visual field as possible, thus overlapping with stimulus presentation. Three additional single pulses were induced to confirm that participants experienced phosphenes, and thus the coil was placed correctly. Halfway through the experiment, participants were blindfolded again, and three single pulses were induced on the mark, to confirm the induction of phosphenes and consequently stable coil placement. During this process, and if necessary, phosphene localization was repeated to adjust for possible drifts.

After localizing the SVC, I estimated each participant's individual threshold by determining the required stimulation power output for perceiving phosphenes using an adjusted staircase method (Cornsweet, 1962). With the use of custom code, double-pulse TMS stimulation was induced on the localised SVC at different stimulation output powers, and participants responded whether they have seen phosphenes or not via button press. Given their responses, the power decreased (if they reported phosphenes twice on a specific TMS power output consecutively) or increased (every time they failed to report phosphenes). Calculations based on the mean of the intervals where the power output changes direction (i.e., from higher power to lower or vice versa) produced an approximation of the stimulation power required to elicit phosphenes 50% of the time the SVC was stimulated. Because this procedure was done with a blindfold over participants eyes, stimulation power in the main experiments was set at 110% of the estimated threshold stimulation power to adjust for visual exposure that can affect the phosphene threshold (Boroojerdi et al., 2000).

To account for individual differences and avoid ceiling or floor effects in task performance, additional procedures were conducted before the main experiments. Specifically, the task was adjusted to each participant's perceptual ability to discriminate between orientation changes. A custom staircase procedure was implemented, where participants had to report whether a grating had a clockwise or counter-clockwise tilt from the horizontal axis. According to each participant's responses, the degrees of this tilt either decreased (when three consecutive correct responses were given) or increased (when a response was incorrect). An approximation of accurately discriminating the orientation difference 75% of the time was obtained by calculating the mean of the intervals where degree differences changed direction (i.e., from an increase in degrees to a decrease and vice versa). The gratings used in this staircase were identical to the experimental stimuli and so this procedure was carried out twice, separately for the blue and red stimuli. For the main experiment, the orientation thresholds both for the red and blue stimuli were increased by 20%, to account for the increased cognitive demands of the main task. Furthermore, before the two main experiments, participants carried out a practice block, based on the results of the orientation discrimination staircase procedure (i.e., individual perceptual ability to discriminate orientation changes) of 24 trials without TMS stimulation to familiarize themselves with the experimental procedure. If accuracy in the practice block was less than 75%, the orientation discrimination staircase and practice block were repeated until the participant reached at least 75% accuracy. Participants were replaced if after four practice blocks their accuracy remained below 75%.

In the main experiment (Figure 4.3), each trial begun with a screen indicating the trial number for each block. To proceed to the next trial, participants needed to press the ‘spacebar’ key on the keyboard. Next, a 500 ms white fixation dot appeared on the centre of a black background, followed by the memory grating for 100 ms. The stimulus grating either had a horizontal orientation (50% of trials), a clockwise (25% of trials) or counter-clockwise (25% of trials) tilt. The tilt angle was fixed across all trials for each participant at the level determined using the staircase procedure described above. From stimulus onset, a 2000 ms delay period indicated by a centred fixation dot followed. Double-pulse TMS were pseudorandomly delivered at one of three different timing conditions after the memory onset; either 0 ms, 200 ms, or 1000 ms. At the end of the delay period, a probe stimulus appeared. In half trials, the probe was the same as the memory array stimulus. In the remaining 50% trials, the probe were different as follows: if the memory array was horizontal, the probe was tilted clockwise (25% of the different-condition trials) or counter-clockwise (25% of the different-condition trials). If the memory array stimulus was tilted, then the probe was horizontal (50% of the different-condition trials). Participants had up to 3000 ms starting at probe onset to respond by placing their index and middle fingers on the arrow keys on the keyboard, indicating whether the orientation of the probe was the same (index finger; ‘left arrow key’) or different (middle finger; ‘down arrow key’) compared to the memory array grating. Feedback was provided only in the cases of no response or an incorrect response, by presenting the word ‘Wrong!’ in red letters in the center of the screen for 1000 ms.

4.2.1.5 Analysis Plan

Analyses were conducted using Jamovi (The Jamovi Project, 2022, Version 2.3.13; https://www.jamovi.org), an openly available R-based statistical software. All data, code, and materials used in this study are available at https://osf.io/d9bqk.

To perform my statistical analyses, I turned to a Bayesian framework. The choice of using Bayesian statistics from hereon, was based on the limitations of the *p*-value and the traditional null hypothesis significance testing (NHST) approach. Specifically, during the past decade, psychology has been intensely criticized as a scientific field, for its less-than-optimal reproducibility (e.g., Derksen, 2019; Nelson et al., 2008; see also Scheel, 2022; Scheel et al., 2021), which introduced the so-called replication crisis of psychology. Partly, this crisis has been attributed to the orthodox use of NHST (Scheel, 2022; Scheel et al., 2021), which is limited by the issues associated with the use of *p*-values, such as its conditioning on the null hypothesis and its inability to quantify evidence (Johansson, 2011; Wagenmakers, 2007). Hence, the crisis facilitated the introduction of Bayesian statistics and the wider use of *BF*s for reaching conclusions in psychological studies (see Dienes, 2014, 2021a; Heck et al., 2022; Kruschke, 2013; Rouder et al., 2009; Schönbrodt & Wagenmakers, 2018; Wagenmakers et al., 2010, 2018). The main argument in favor of a Bayesian approach over the conventional frequentist approach, is the advantage of a *BF* to quantify evidence in favor of either the alternative or the null hypotheses (Dienes, 2014; Dienes & Mclatchie, 2018; van Ravenzwaaij, & Etz, 2021), contrary to the *p*-value, which can only provide information about the rejection of the null hypothesis (Johansson, 2011; Wagenmakers, 2007).

Put simply, the *BF* is a ratio that reflects the likelihood of one model (e.g., the alternative hypothesis: H_1) over another (e.g., the null hypothesis: H_0). Often, the *BF* is denoted "BF_{10}" to indicate the likelihood of the alternative hypothesis over the null hypothesis, and, respectively, "BF_{01}" to signify the ratio of the null hypothesis over the alternative hypothesis (Dienes, 2019, 2021b; Dienes & Mclatchie, 2018; van Doorn et al., 2021; van Ravenzwaaij, & Etz, 2021). For example, a $BF_{10} = 3$, indicates that it is three times more likely for the data to have been observed under the alternative hypothesis, and respectively, a $BF_{10} = 0.3$ shows that it is three times more likely that the data have been observed under the null hypothesis. To calculate the *BF,* statistical models are built that reflect the expected probabilities for each hypothesis (prior probabilities), along with the anticipated distributions for each model parameter (prior distributions). Next, the observed data are fit into these models and provide estimates for parameters of the model (posterior distribution), and a *BF* can be produced by comparing the posterior to the prior distributions (see Heck et al., 2022; Wagenmakers et al., 2010), according to Bayes Theorem (for examples see van Ravenzwaaij, & Etz, 2021; see also Kruschke, 2013; Rouder et al., 2009). Also, this property makes the *BF* is an updatable ratio (hence it is often referred to as the *predictive updating factor;* Schönbrodt & Wagenmakers, 2018), which means that as additional data are accumulated, the evidence in favor of the most probable hypothesis, reflected by the *BF*, increases (Fu et al., 2021; Schönbrodt et al., 2017; Schönbrodt & Wagenmakers, 2018;

van Ravenzwaaij & Etz, 2021; Wagenmakers et al., 2010). Therefore, researchers are not necessarily depended upon an a-priori determined sample size, but can continue collecting data, until enough evidence has been obtained (i.e., when the *BF* reaches a predefined threshold) (Fu et al., 2021; Schönbrodt et al., 2017; Schönbrodt & Wagenmakers, 2018; van Ravenzwaaij & Etz, 2021; Wagenmakers et al., 2010), as was implemented here with the sequential procedure. Accordingly, to support their conclusions, researchers define a *BF* threshold value (X), which needs to be exceeded so that evidence can be considered substantially in favor of either the alternative (BF_{10} > X) or the null (BF_{10} < 1/X) hypothesis (Brysbaert, 2019; Palfi & Dienes, 2020; Wagenmakers et al., 2010). Because of the advantage of the *BF* to quantify evidence for either the null or the alternative hypothesis, I have espoused Bayesian statistics for my analyses in all following experiments.

The TMS site (ipsilateral vs. contralateral) was the independent variable in Experiment 1. Since monocular vision was ensured, the ipsilateral condition refers to the situation where the TMS localised site (for example, right SVC) was on the same side as the eye processing the stimulus (for example, right eye, and consequently the blue stimulus). The contralateral condition corresponds to when the TMS localised site (for example, right SVC) did not match the side of the eye processing the stimuli (for example, left eye, and consequently red stimulus).

The main dependent variable that was considered is d'. The d' variable is a signal detection theory indicator of detection sensitivity calculated by subtracting the standardised false alarm rate of responses from the standardised hit rate:

$$d' = z(H) - z(FA)$$

where *H* is the Hit rate (i.e., correct responses of the probe being the same as the memory array grating) and *FA* is the False Alarm rate (i.e., incorrect responses of the probe being the same as the memory array grating). These rates correspond to probabilities on the normal distribution, therefore *z(H)* and *z(FA)* are the *z*-scores that correspond to the normal distribution's tail *p*-values represented by *H* and *FA*.

In Experiment 1, I performed three Bayesian paired *t*-tests to calculate a Bayes Factor; one *t*-test on TMS stimulation site (ipsilateral d' vs. contralateral d') for each of the three TMS timing conditions (0 ms, 200 ms, 1000 ms). Each t-test examined if the difference between the ipsilateral *d'* and contralateral *d'* differs from zero. The Bayes Factor indicated the likelihood ratio of each alternative hypothesis over the null hypothesis (BF_{10}), thus providing evidence for the likelihood of both hypotheses. The 0 ms timing condition worked as an outcome neutral test or positive control condition, in order to test my methods. Given that the effect of TMS might affect both hemispheres and/or that the SVC processes information in both hemispheres through feedforward and feedback processes, it is possible that TMS effects between hemispheres remained undetected with my proposed methods. This possibility was tested in Experiment 2, with the introduction of sham TMS condition and statistical tests between real versus sham TMS across hemispheres. The 200 ms and 1000 ms timing conditions tested whether the SVC is involved during early and late maintenance of visual information, respectively.

Each prior for the paired *t*-tests was described by a Cauchy distribution centered around zero (see Rouder et al., 2009). Each prior was based on the results of the meta-analysis in Chapter 3. The standardized differences were used to inform the width parameter of each Cauchy prior. In detail, by considering the overall effect size (g = .58), the effect size for early TMS (up to 200 ms; g = .80), and the effect size for late TMS (after 200 ms; g = .50) from Chapter 3, the width parameter of the Cauchy distribution corresponded to 0.58 for the 0 ms condition, to 0.8 for the 200 ms condition, and to 0.5 for the 1000 ms condition, respectively.

Participants with an overall accuracy in the experimental trials close to chance levels (< 60% accuracy) in Experiments 1 were excluded from analyses and replaced. The data of such participants were not used during Bayesian sample updating nor for my main analyses. Additionally, I excluded and replaced participants in the case of technical or other difficulties, if data loss was greater than 20% of the total experimental trials. Further, the slowest and fastest responses were removed from the analyses. To do so, I filtered each participant's responses and excluded any data that concerned response times that were further than 3 standard deviations (*sd*) away from each participant's mean reaction time. Assuming that the reaction times of each participant are normally distributed, I expected less than 0.5% of the data of each participant to be excluded from the main analyses.

4.2.2 Results

4.2.2.1 Main Hypotheses

The 36 participants in Experiment 1 averaged 71.7% (*sd* = 6.1%) overall accuracy for the VSTM task. Filtering the reaction times that were 3 *sd*s further away from each participant's mean reaction time excluded on average 3.5% (*sd* = .64%) of trials. Following the SVC localization approach described previously (see *4.2.1.4 Procedure*), phosphene induction was successful for 25 participants, who had an average phosphene threshold of 66.2% (*sd* = 16.5%) out of the total (100%) stimulation power of the Magstim Super Rapid^2 stimulator. For participants who failed to perceive phosphenes a fixed power set at 65% of the stimulator maximum output was used, with the coil placed approximately 2 cm above and 0.5 cm laterally, as previously discussed (see *4.2.1.4 Procedure*). The TMS coil was placed on the right hemisphere of 19 participants and on the left hemisphere of the remaining 17 participants.

Experiment 1 focused on three main hypotheses, which aimed to investigate the role of the SVC, by comparing the ipsilateral (experimental) to the contralateral (control) TMS site conditions, during three different VSTM phases, as follows: perceptual processing (H1), early visual information maintenance (H2), and late visual information maintenance (H3). The results of my main analyses concerning Experiment 1 are summarised in Table 4.1 and presented visually in Figure 4.4.

For H1 the Bayesian paired *t*-test on mean *d'* regarding the outcome neutral (positive control) condition (0 ms TMS timing condition; Figure 4.4B) revealed that the methods implemented in Experiment 1 were adequate to test for differences between the ipsilateral and contralateral conditions (BF_{10} = 29.40). This was reflected by a decrease in mean *d'* in the ipsilateral (mean *d'* = .95, *sd* = .61) compared to the contralateral (mean *d'* = 1.56, *sd* = .78) 0 ms TMS timing condition. This finding replicates the expected, consistent, inhibitory effect on VSTM performance due to SVC TMS during visual perception processes (for a review see de Graaf et al., 2014; Chapter 2, Chapter 3). Further, robustness analyses revealed that evidence, as reflected by the BF_{10}, remains above the predefined threshold (BF_{10} > 3) for various prior distribution widths, including narrow (*r* = .3), wide (*r* = 1), and ultrawide (*r* = 1.5) scale widths (Figure 4.2A). As such, these results are in line with my H1, where a difference between the ipsilateral and contralateral conditions was anticipated when SVC TMS is induced at 0 ms, thus confirming the essential role of SVC processes during perception.

Table 4. 1: Data and analyses concerning the analyses of Experiment 1 ($n = 36$).

Hypothesis	**TMS Timing**	**TMS site**	**Mean (*sd*) *d'***	**Bayes Factor (BF_{10})**
H1	0 ms	Ipsilateral	0.95 (0.61)	29.40
		Contralateral	1.56 (0.78)	
H2	200 ms	Ipsilateral	1.11 (0.59)	35.99
		Contralateral	1.65 (0.75)	
H3	1000 ms	Ipsilateral	0.99 (0.69)	3.67
		Contralateral	1.45 (0.67)	

Notes. TMS; transcranial magnetic stimulation.

Evidence for a similar inhibitory effect was found for H2 (Figure 4.4C), which explored the early maintenance of visual information during VSTM that was reflected in the 200 ms TMS timing condition. In detail, the Bayesian paired *t*-test for the 200 ms TMS timing condition (early VSTM maintenance processes), indicated that mean *d'* was decreased in the ipsilateral (mean $d' = 1.11$, $sd = .59$) compared to the contralateral (mean $d' = 1.65$, $sd = .75$) condition ($BF_{10} = 35.99$). As indicated by the robustness analyses, the BF_{10} was consistently above the threshold ($BF_{10} > 3$) for narrow ($r = .3$), wide ($r = 1$), and ultrawide ($r = 1.5$) prior scale widths (Figure 4.2B). Here, I hypothesised that evidence for a difference between the ipsilateral and contralateral conditions will be found when SVC TMS is induced at 200 ms. Aligned with H2, the results indicated the presence of a difference, therefore confirmed the involvement of the SVC during the early maintenance of visual information.

Analogous effects of reduced VSTM performance were found for H3 that concerned the late maintenance of visual information during VSTM (Figure 4.4D); a condition that was echoed in the 1000 ms TMS timing condition. The Bayesian paired *t*-test for the 1000 ms TMS timing condition (late VSTM maintenance processes) revealed a decrease in mean *d'* when comparing the ipsilateral (mean $d' = .99$, $sd = .69$) with the contralateral (mean $d' = 1.45$, $sd = .67$) conditions ($BF_{10} = 3.67$). The robustness analyses showed that the threshold ($BF_{10} > 3$) was surpassed for a narrow prior ($r = .3$), but not for a wide ($r = 1$; $BF_{10} = 2.59$) and ultrawide ($r = 1.5$; $BF_{10} = 1.9$) prior (Figure

4.2C). Despite not reaching the threshold for wider priors, the BF_{10} still indicates greater likelihood for the alternative hypothesis, thus favoring the presence of a difference, with an increasing trend as more participants are included. As with the previous hypotheses, the results for H3 were consistent with my hypothesis that evidence of a difference between the ipsilateral and contralateral conditions will be present when SVC TMS is induced at 1000 ms. Hence, this evidence supports the involvement of the SVC during the late maintenance of visual information during VSTM.

Figure 4. 4: Results for Experiment 1 with 36 participants.

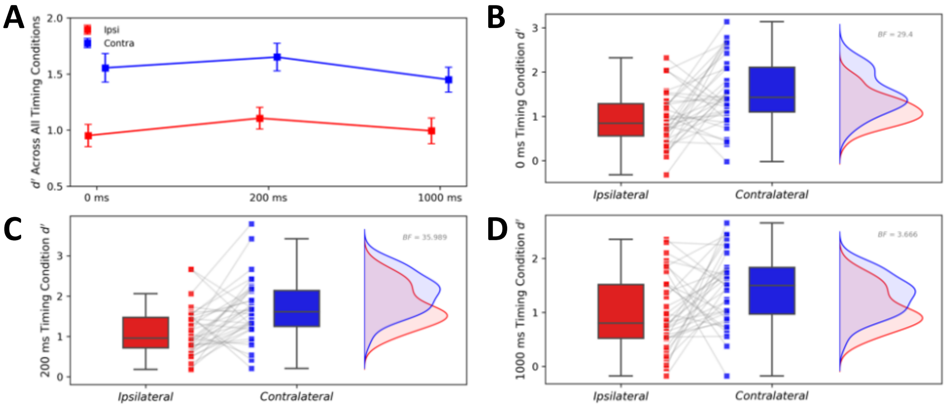


Fig.4.4. Detection sensitivity (*d'*) in Experiment 1 VSTM task performance across different TMS site coil placement and timing conditions. Because of monocular stimulus presentation, ipsilateral TMS (red) serves as the experimental condition, while contralateral TMS (blue) is the control condition. Mean *d'* is presented for (A) all timing conditions. Mean and individual *d'* scores are illustrated for (B) the 0 ms (outcome neutral), (C) the 200 ms (early VSTM maintenance), and (D) the 1000 ms (late VSTM maintenance) conditions.

Notes. TMS; transcranial magnetic stimulation, VSTM; visual short-term memory.

4.2.2.2 Exploratory Analyses

Exploratory analyses were performed using the JASP statistical software package (JASP Team, 2022, Version 0.16.3; https://jasp-stats.org). Of note, to compute Bayesian analyses, Jamovi uses a JASP based package, thus I anticipate that results are consistent between the two statistical packages. The exploratory repeated measures analysis of variance (rmANOVA) tests were informed using the priors suggested by Rouder et al. (2012), which assume Cauchy distributions centered on 0 (fixed effects $r = .5$; random effects $r = 1$). For the exploratory *t*-test, I used a Cauchy distribution centered on 0 with a width set to 0.58, based on the overall TMS effect that was found in Chapter 3.

Previous studies have reported different TMS effects across stimulation sites for the different stimulation timing conditions (Rademaker et al., 2017; van de Ven et al., 2012; van Lamsweerde et al., 2017). To explore these effects for Experiment 1, I conducted a Bayesian rmANOVA for the TMS site and TMS timing conditions. This created a two (ipsilateral vs contralateral) by three (0 ms, 200 ms, 1000 ms) model (Figure 4.4A). To explore the model that better represents the data, I conducted analysis on the factor effects by calculating the likelihood ratio representing the change from prior odds to posterior odds for each factor in the model averaged by all the models that include each factor (BF_{incl}). The BF_{incl} for all factors and interactions are provided in Table 4.2. In detail, the inclusion of the TMS site factor resulted in the highest BF_{incl} ($BF_{incl} = 23.01$). Also, there was moderate evidence against the inclusion of an interaction of TMS site and TMS timing ($BF_{incl} = .34$), however, the inclusion of the TMS timing factor resulted in indecisive evidence ($BF_{incl} = .73$). The results of the exploratory Bayesian rmANOVA inform that, in line with the registered analyses of Experiment 1, a TMS site (ipsilateral vs contralateral) effect is evident and that an interaction with TMS timing is unlikely.

Table 4. 2: Experiment 1 (*n = 36*) Bayesian repeated measures ANOVA results.

Model	**Bayes Factor (BF_{incl})**
TMS Site	23.01
TMS Time	0.73
TMS Site * TMS Time	0.34

Notes. BF_{incl} is calculated as the likelihood ratio representing the change from prior odds to posterior odds for each factor in the model averaged by all the models that include each factor. TMS; transcranial magnetic stimulation.

Taken together, these results support the involvement of the SVC during VSTM. Further to the inhibitory effects found in the outcome neutral condition, which confirmed the reliability of my methods, the inhibitory TMS effects observed during the 200 ms and 1000 ms stimulation timing conditions, signify the involvement of the SVC during early and late VSTM maintenance. However, it is possible that due to feedforward and feedback (or other) mechanisms (Gibaldi et al., 2021; King & Wyart, 2021; Zhao et al., 2021), the information is in reality passed to the contralateral hemisphere, and instead the inhibitory TMS effect is a misinterpretation of a truly facilitation effect. To investigate this possibility, in my second experiment, which I describe next, I introduced sham TMS.

4.3 Experiment 2: Sham and Real Transcranial Magnetic Stimulation of the Sensory Visual Cortex During Visual Short-Term Memory

Experiment 2 aimed to replicate the effects that were obtained in Experiment 1, while controlling for other factors that may cause or hinder my experimental effects, by adding a sham-TMS control condition. In addition to controlling for TMS noise and other artefacts, a sham TMS control is important for three reasons. First, TMS interference may affect both hemispheres due to the visual input being processed by both hemispheres and thus any actual effects remain undetected (de Graaf & Sack, 2011; Pitcher et al., 2020). Since Experiment 1 compared an ipsilateral with a contralateral condition, where stimulation is always present, it is plausible that TMS noise interferes in such a way, that an effect in behaviour is always present. Thus, if the additional noise by TMS affects the baseline condition, then comparisons between the ipsilateral and contralateral stimulation condition might not indicate any reliable difference. By introducing a sham TMS condition, Experiment 2 controlled for this possibility, allowing comparisons between real and sham stimulation. Second, it is likely that the SVC processes information in both hemispheres (e.g., due to feedforward and feedback mechanisms; King & Wyart, 2021; Zhao et al., 2021) so that stimulating only one of the two hemispheres is not enough to affect behavioural measures. Lastly, contrary to previous research, I suggested that visual information was initially processed by the ipsilateral SVC when the stimulus was presented within approximately 15° of visual angle from midline (Joukal, 2017; Tong et al., 2006; Wichmann & Müller-Forell, 2004). However, without a sham control condition, it would be impossible to correctly interpret the direction of any possible effect. Specifically, in previous experiments, TMS was shown to either facilitate (Cattaneo et al., 2009) or hinder (Jia et al., 2021; van de Ven et al., 2012) performance. It should be pointed out, that the interpretations of such effects are unavoidably biased by the hypotheses. For example, if an effect is expected in the contralateral site, an increased performance might be interpreted as a facilitation effect but might, in reality, be due to hindering effects in the ipsilateral condition. Thus, given the neural basis of the visual pathway (Gibaldi et al., 2021; Joukal, 2017; Tong et al., 2006; Wichmann & Müller-Forell, 2004), along with the possible feedforward and feedback mechanisms of the SVC (e.g., Miller et al., 1996; Van Kerkoerle et al., 2017; see also King & Wyart, 2019), this is an important factor that must be controlled for. Therefore, Experiment 2, allowed comparisons between actual and sham stimulation on behaviour.

4.3.1 Methods

The hypotheses and methods of Experiment 2 were included in the same preregistered report of Experiment 1, which received in principle acceptance on 06 June 2022 after undergoing peer review from Peer Community in Registered Reports. The accepted Stage 1 protocol can be accessed at https://doi.org/10.17605/OSF.IO/EMPDT.

4.3.1.1 Participants

A similar, to that of Experiment 1, sample updating process with a stopping rule ($BF_{10} > 3$ or $< 1/3$) was set for all four paired *t*-tests of Experiment 2. A minimum of 20 participants (to ensure counterbalancing) or a maximum of 40 participants (due to constraints) were to be recruited for Experiment 2.

In Experiment 2 data collection was stopped, according to my sequential procedure, after collecting data from 28 (24 females) participants (Figure 4.5) with mean age 20.29 (*sd* = 3.14) years. Thirty-two participants were recruited in total for Experiment 2, however, as per my preregistered sampling plan three participants were replaced because of poor VSTM task performance (accuracy < 60%) and one participant was replaced due to self-reported history of amblyopia during study debriefing. The results from the participants that were replaced were not included in any of the analyses.

4.3.1.2 Apparatus and Stimuli

The same apparatus and stimuli as in Experiment 1 were used in Experiment 2. Additionally, in Experiment 2, a sham coil was used to control for noise and other TMS artefacts. The sham coil looks identical to the D70 Alpha Flat Coil, but it is equipped with thicker shield, restricting it from inducing magnetic fields that interfere with brain activity.

Figure 4. 5: Sequential and prior robustness analysis for Experiment 2.

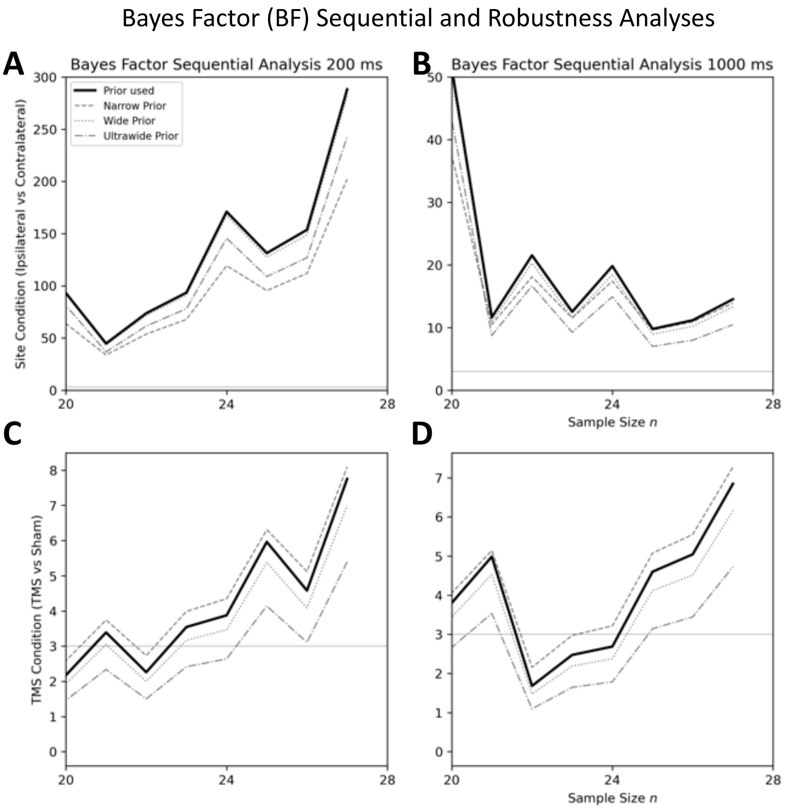


Fig.4.5. Bayes Factor (*BF*) sequential and robustness analysis for TMS site (ipsilateral vs contralateral) in the (A) 200 ms and (B) 1000 ms timing conditions, and for the TMS condition (real vs sham) in the (C) 200 ms and (D) 1000 ms timing conditions. Following my stopping rule, data collection in Experiment 2 stopped at 28 participants, when the predefined *BF* threshold (*BF* > 3; presented here as the grey horizontal solid line) was reached for all three registered analyses. The *BF* sequential analysis for each registered analysis is shown with a black solid line. The *BF* was informed by a Cauchy distribution centered on 0 with a scaling factor set to (A, C) r = .8 and (B, D) r = .5. To test the robustness of the *BF*, analyses were repeated for a narrow prior with r = .3 (dashed grey line), a wide prior with r = 1 (dotted grey line), and an ultrawide prior with r = 1.5 (dash-dotted grey line).

Notes. TMS; transcranial magnetic stimulation.

4.3.1.3 Experimental Design

The same delayed change-detection VSTM task as in Experiment 1 was used here (see *4.2.1.2 Apparatus and Stimuli*). Though, since sham TMS was introduced in Experiment 2, which worked as a baseline measurement, the 0 ms condition that was used as an outcome neutral condition in Experiment 1 was dropped. Therefore, in Experiment 2, only two timing conditions were used, at 200 ms (first TMS pulse at 200 ms after stimulus onset and second TMS pulse at 300 ms after stimulus onset) and 1000 ms (first TMS pulse at 1000 ms after stimulus onset and second TMS pulse at 1100 ms after stimulus onset), corresponding to an early maintenance phase and a late maintenance phase of VSTM respectively. As in Experiment 1, the timing conditions refer to the temporal distance between stimulation and memory array onset. This lead to a within-subject design, comparing differences between the ipsilateral and contralateral conditions, at two different TMS timing conditions, and two different stimulation conditions. These conditions created a two (ipsilateral/contralateral) by two (200 ms/1000 ms) by two (TMS/sham TMS) design. In total, 576 trials (288 TMS conditions; 144 per timing condition out of which 72 ipsilaterally and 72 contralaterally and 288 sham TMS conditions; 144 per timing condition 72 ipsilaterally and 72 contralaterally) were collected, which were divided into eight blocks of 72 trials and presented across participants in a counterbalanced fashion.

4.3.1.4 Procedure

The procedure in Experiment 2 was identical to Experiment 1 (see *4.2.1.4 Procedure*). The only difference in Experiment 2 is the introduction of a sham coil that delivered sham stimulation. TMS and sham TMS conditions were blocked in a counterbalanced order. In addition, given the sham TMS condition, the 0 ms condition of Experiment 1 that acted as an outcome neutral test, was dropped. At the end of Experiment 2, participants self-reported whether they noticed any differences between sham TMS and TMS.

4.3.1.5 Analysis Plan

In Experiment 2, the independent variables were the stimulation site (ipsilateral, contralateral) and the TMS condition (real, sham). As in Experiment 1 (see *4.2.1.5 Analysis Plan*), the dependent variable was the estimated detection sensitivity as measured with *d’*. Thus, for Experiment 2 I performed four paired *t*-tests; one *t*-test between ipsilateral *d’* versus contralateral *d’* for each of the two TMS timing conditions (200 ms, 1000 ms) only for the real TMS condition, and one paired *t*-test between real TMS *d’* versus sham TMS *d’* for each of the TMS timing conditions (200 ms, 1000 ms) across hemispheres. The stimulation site (ipsilateral vs. contralateral) *t*-test was performed to replicate the results of Experiment 1 regarding the involvement of the SVC during early (200 ms condition paired *t*-test) and late (1000 ms condition paired *t*-test) VSTM maintenance, by testing if the difference between ipsilateral *d’* and contralateral *d'* equalled to 0 (null hypothesis) or not (alternative hypothesis). The real TMS *d'* versus sham TMS *d'* comparison tested the effects of stimulation across hemispheres to provide evidence for the involvement of the SVC during early (200 ms condition paired *t*-test) and late (1000 ms condition paired *t*-test) VSTM maintenance, by testing if the difference between real TMS *d'* and sham TMS *d'* equalled to 0 (null hypothesis) or not (alternative hypothesis). Further, it indicated whether the analyses between the stimulation site (ipsilateral vs. contralateral) were insufficient to detect a TMS effect (e.g., if evidence was found in favor of the null hypotheses for ipsilateral vs. contralateral tests and evidence for an alternative hypothesis was found in the real TMS vs. sham TMS tests), or if the SVC is not involved during early and/or late VSTM maintenance (evidence in favor of the null hypotheses in both ipsilateral vs. contralateral and real vs. sham TMS tests).

The priors which were used for the paired t-tests were described as a Cauchy distribution centered around 0 with a width set to 0.8 for the 200 ms condition and 0.5 for the 1000 ms condition, as estimated by the results of the meta-analytic evidence in Chapter 3, which reported the standardised effect size for early TMS (up to 200 ms; g = .8) and for late TMS (after 200 ms; g = .5).

4.3.2 Results

4.3.2.1 Main Hypotheses

The average overall accuracy in the VSTM task of Experiment 2 of the 28 participants was 71.5% (*sd* = 6.6%). Reaction time filtering (excluding trials with reaction times 3 *sd*s further from each participant's mean reaction time) resulted in the exclusion of 3.7% (*sd* = .86%) of trials, on average, for each participant. Phosphene induction was successful for 18 participants with an average phosphene threshold of 54.5% (*sd* = 21.8%). As in Experiment 1, a fixed output power set at 65% was used, with the coil placed approximately 2 cm above and 0.5 cm laterally, for participants who failed to perceive phosphenes (see *4.2.1.4 Procedure*). For 15 participants, the coil was placed on the right hemisphere.

Four main hypotheses were tested in Experiment 2, which introduced sham stimulation. Two hypotheses concerned replicating the findings of Experiment 1 for early (H4) and late (H6) VSTM maintenance. To replicate the previous findings (H2 and H3 of

Experiment 1), data from the sham TMS conditions were excluded from the analyses pertaining to H4 and H6. The remaining two hypotheses examined the role of the SVC by comparing real with sham stimulation during early (H5) and late (H7) stimulation. The results of the registered analyses of Experiment 2 are summarized in Table 4.3 and presented in Figure 4.6.

The results related to H4 replicated my findings from Experiment 1 regarding the involvement of the SVC during the early maintenance of visual information in VSTM (Figure 4.6B). The Bayesian paired t-test showed that when real TMS is induced at 200 ms the ipsilateral (mean $d' = .72$, $sd = .76$) compared to the contralateral (mean $d' = 1.65$, $sd = .69$) mean d' is decreased ($BF_{10} = 288.18$). The BF_{10} remained consistently above the threshold ($BF_{10} > 3$) for narrow ($r = .3$), wide ($r = 1$), and ultrawide ($r = 1.5$) prior scale widths according to robustness analyses (Figure 4.5A). This result replicates the findings of Experiment 1 (H2), and further strengthens my hypothesis that the SVC is a necessary component of VSTM involved in the early maintenance of visual information.

Further, I analysed the differences between sham and real stimulation for the 200 ms TMS timing condition (H5; Figure 4.6C). As previously described, this analysis was aimed to investigate the involvement of the SVC in VSTM maintenance, in case the ipsilateral and contralateral comparisons were insufficient to do so, and to confirm the direction of the TMS effects (inhibitory vs. facilitatory). These analyses were performed across the brain hemispheres, independent of the coil placement condition (i.e., without considering the ipsilateral or contralateral conditions). The results of the Bayesian paired t-test indicated that mean d' was reduced in the real TMS (mean $d' = 1.08$, $sd = .44$) compared to the sham TMS (mean $d' = 1.3$, $sd = .54$) condition ($BF_{10} = 7.75$), an effect that remained robust over the threshold ($BF_{10} > 3$) across a narrow ($r = .3$), wide ($r = 1$), and ultrawide ($r = 1.5$) prior (Figure 4.5B). In addition to strengthening the evidence in favor of the involvement of the SVC in early VSTM maintenance, this finding confirms the inhibitory effects of TMS induced at 200 ms, which were evident by the ipsilateral and contralateral comparisons (H2 and H4).

Table 4. 3: Data and analyses concerning the analyses of Experiment 2 (*n = 28*).

Hypothesis	TMS Timing	TMS site	Mean (*sd*) *d'*	Bayes Factor (BF_{10})
H4	200 ms	Ipsilateral (TMS only)	0.72 (0.76)	288.18
		Contralateral (TMS only)	1.66 (0.69)	
H5	1000 ms	Ipsilateral (TMS only)	0.85 (0.80)	15.49
		Contralateral (TMS only)	1.59 (0.75)	
H6	200 ms	TMS	1.08 (0.44)	7.75
		Sham	1.30 (0.54	
H7	200 ms	TMS	1.11 (0.46)	3.67
		Sham	1.31 (0.45)	

Notes. TMS; transcranial magnetic stimulation.

As for the late maintenance of visual information, I initially tested for differences between the ipsilateral and contralateral TMS conditions when stimulation was induced at 1000 ms (H6; Figure 4.6E) and once again replicated the results of Experiment 1. Specifically, evidence for a difference was provided by the Bayesian paired *t*-test, showing decreased *d'* for the ipsilateral (mean *d'* = .85, *sd* = .8) compared to the contralateral (mean *d'* = 1.59, *sd* = .75) condition (BF_{10} = 10.84). Robustness analyses showed that the BF_{10} surpassed the threshold ($BF_{10} > 3$) for priors with narrow ($r = .3$), wide ($r = 1$), and ultrawide ($r = 1.5$) widths (Figure 4.5C). As was the case with early maintenance, results for H6 replicated the effect that was found in Experiment 1 and provided additional evidence for the involvement of the SVC during late VSTM information maintenance.

For the final main hypothesis, H7, I investigated the 1000 ms TMS timing condition for differences between sham and real stimulation (Figure 4.6F). As indicated by the Bayesian paired *t*-test, mean *d'* in the real TMS condition (mean *d'* = 1.11 *sd* = .46) was decreased in comparison with the sham TMS (mean *d'* = 1.34, *sd* = .45) condition (BF_{10} = 8.39). The BF_{10} threshold ($BF_{10} > 3$), was exceeded for narrow ($r = .3$), wide ($r = 1$), and ultrawide ($r = 1.5$) prior widths, as reflected by robustness analyses (Figure 4.5D). This finding, offers additional evidence for the involvement of the SVC in late VSTM maintenance, and provides further support for the inhibitory TMS effects, as was the case with the ipsilateral and contralateral comparisons for stimulation induced at 1000 ms (H3 and H6).

Figure 4. 6: Results for Experiment 2 with 28 participants.

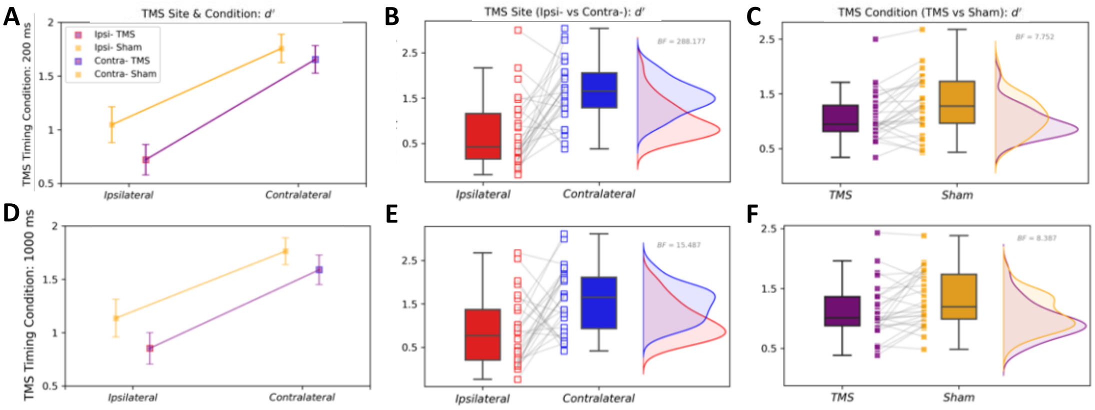


Fig.4.6. Detection sensitivity (*d'*) in Experiment 2 VSTM task performance across different TMS and sham conditions, different site coil placement, and different timing conditions. For the 200 ms condition (left pane) mean *d'* are shown for (A) both real (purple) and sham (orange) TMS, for the ipsilateral (red) and contralateral (blue) conditions. (B) Mean and individual *d'* scores between the ipsilateral and contralateral 200 ms conditions are shown only for the real TMS condition. (C) Mean and individual *d'* scores between sham and real TMS across hemispheres in the 200 ms condition. Results for the 1000 ms condition are illustrated in the right pane. Mean *d'* for (D) real and sham TMS, for the ipsilateral and contralateral conditions. Mean and individual *d'* scores for the 1000 ms condition between (E) the ipsilateral and contralateral coil placement, and between (F) real and sham stimulation.

Notes. TMS; transcranial magnetic stimulation, VSTM; visual short-term memory.

4.3.2.2 Exploratory Analyses

A Bayesian rmANOVA was implemented to explore the possible effects across the TMS condition, site, timing factors. In detail, I explored a two (real vs sham) by two (ipsilateral vs contralateral) by two (200 ms, 1000 ms) model (Figures 6A and 6D). As with Experiment 1, I performed an analysis of effects by calculating a BF_{incl} for each factor and interaction included in the model. The BF_{incl} resulting from this analysis are presented in Table 4.4. Specifically, the highest BF_{incl} was produced by the TMS condition model ($BF_{incl} = 31.45$), followed by that of the TMS site model ($BF_{incl} = 15.45$). The models including solely TMS timing, or TMS timing interactions resulted in low BF_{incl} (all $BF_{incl} < .37$; see Table 4.4 for details), thus providing moderate to strong evidence against any timing effects or interactions. The results of the Bayesian rmANOVA are analogous to those registered for Experiment 2, where both a TMS condition (sham vs real) and TMS site (ipsilateral vs contralateral) effects were found, but differences across timings are unlikely.

To further explore the effects of the TMS condition and the TMS site factors, I performed post-hoc Bayesian paired *t*-tests. Evidence for an overall real compared to sham TMS was found ($BF_{10} = 60.5$), signifying impaired performance in the real TMS (mean $d' = 1.09$, $sd = .42$) compared to the sham TMS (mean $d' = 1.29$, $sd = .91$) condition. This was an expected finding considering the inhibitory effects that were confirmed through my registered analyses. Further, an overall ipsilateral versus contralateral difference was shown ($BF_{10} = 41.85$), indicating that overall performance in the ipsilateral condition (mean $d' = .91$, $sd = .76$) was worse compared to the contralateral condition (mean $d' = 1.65$, $sd = .62$). This overall TMS site (ipsilateral vs contralateral) effect is likely attributed to the consistent stimulation of one brain hemisphere, which can lead to perceptual inhibition (de Graaf et al., 2014; Tapia et al., 2014). A deeper investigation into these factors showed that the real versus sham effects are evident only in the ipsilateral conditions in both the 200 ms (ipsilateral TMS mean $d' = .72$, $sd = .76$, ipsilateral sham mean $d' = 1.05$, $sd = .89$, $BF_{10} = 6.67$) and the 1000 ms (ipsilateral TMS mean $d' = .85$, $sd = .8$, ipsilateral sham mean $d' = 1.14$, $sd = .95$, $BF_{10} = 3.02$) timing conditions. Real versus sham TMS comparisons in the contralateral condition remained inconclusive for the 200 ms (contralateral TMS mean $d' = 1.66$, $sd = .69$, contralateral sham mean $d' = 1.76$, $sd = .71$, $BF_{10} = .4$) and 1000 ms (contralateral TMS mean $d' = 1.59$, $sd = .75$, contralateral sham mean $d' = 1.76$, $sd = .68$, $BF_{10} = 1.56$) timing conditions, since the BF_{10} failed to reach my predefined threshold ($1/3 < BF_{10} < 3$).

In general, the results from Experiment 2 replicate the findings of Experiment 1 and strengthened the evidence in favor of the involvement of the SVC during VSTM maintenance. The introduction of a sham condition upheld the inhibitory TMS effects that were also found in the ipsilateral versus the contralateral comparisons, which indicates that SVC TMS during the VSTM maintenance period impairs VSTM performance. Overall, since TMS disrupted early and late VSTM maintenance processes, my findings are aligned with the sensory recruitment hypothesis. In the following section, I discuss some exploratory analyses.

Table 4. 4: Experiment 2 (*n = 28*) Bayesian repeated measures ANOVA results.

Model	**Bayes Factor (*BF_{incl}*)**
TMS condition	31.45
TMS site	15.45
TMS condition x TMS site	1.73
TMS time	0.21
TMS condition x TMS time	0.18
TMS site x TMS time	0.36
TMS condition x TMS site x TMS time	0.08

Notes. BF_{incl} is calculated as the likelihood ratio representing the change from prior odds to posterior odds for each factor in the model averaged by all the models that include each factor. TMS; transcranial magnetic stimulation.

4.4 Chapter 4 Summary

The aim of Chapter 4 was to investigate if SVC is a necessary component of the brain network involved in the short-term maintenance or storage of visual information. For this reason, my experimental methods were designed for overcoming methodological issues that were identified in previous TMS studies investigating similar questions (see Chapter 2). Overcoming these oversights required the monocular presentation of stimuli, and the use of stimuli comprised of elemental visual features, such as orientation. In two experiments, I showed that TMS impairs VSTM task performance when induced during both early (200 ms) and late (1000 ms) visual information maintenance. The reliability of my methods, which were preregistered prior to any data collection, were confirmed by similar inhibitory TMS effects found during perception (outcome neutral condition; Experiment 1) and by sham TMS performance comparisons (Experiment 2). These results provide causal evidence for the involvement of the SVC in VSTM maintenance, in line with the sensory recruitment framework. In Chapter 5 that follows, I turn to a different manipulation, which is memory load, to further investigate the sensory recruitment framework.

5 Evidence for Visual but not Auditory Modality Specific Sensory Recruitment from Memory Load Manipulation

5.1 Chapter 5 Introduction

Following the causal evidence for sensory recruitment during VSTM provided by the TMS experiments (see Chapters 2, 3, 4), I now turn to explore sensory recruitment through a different manipulation method. Specifically, in the present chapter, I manipulate memory load to provide additional evidence of sensory recruitment during VSTM and explore whether similar evidence holds for the auditory modality.

As discussed in Chapter 1 (see *1.3.1.1 Behavioral and Psychophysical Experiments*), previous studies have utilized VSTM load manipulations to explore the relationship between VSTM and visual perception. In detail, studies showed that by taxing VSTM capacity, the detection of irrelevant stimuli that are presented outside the focus of attention during the delay period of a VSTM task is reduced (Konstantinou & Lavie 2013) and so is the interference by distractors (Konstantinou et al., 2014). These findings were specific to sensory load and different for other types of cognitive load, such as verbal WM tasks (Konstantinou & Lavie 2013; Konstantinou et al., 2014), which point towards a shared neural mechanism for both the memory and perception of visual stimuli, as proposed by the sensory recruitment framework (Pasternak & Greenlee, 2005; Lorenc & Sreenivasan, 2021; Teng & Postle, 2021).

Subsequent studies have elucidated on this shared neural mechanism and provided additional support for sensory recruitment. For example, psychophysical work showed that the VSTM load effects on the perception of irrelevant contrast stimuli results on horizontal shift of the contrast response function, which corresponds to a contrast gain effect that attributes the effects to changes in sensory input (Konstantinou & Lavie, 2020). As for fMRI data, Konstantinou et al. (2010, 2012) found a decrease on BOLD signal activity for a contrast stimulus presented at periphery, during the delay period of a VSTM task under a high memory load condition, compared to a low memory load condition.

Despite the findings indicating that VSTM load impairs perceptual processing within the visual domain (Lavie et al., 2014; Konstantinou et al., 2010, 2012, 2014;

Konstantinou & Lavie, 2013, 2020), assuming the distributed VSTM view it still remains unclear how sensory-specific memory load interacts with perceptual input cross-modally (e.g., across the visual and auditory domain). For example, it is still questionable if sensory-specific capacity limitations depend upon a common neural mechanism (e.g., attentional demand), and therefore resources are shared between modalities, or if each modality is characterised by its modality-specific resources (see Shevlin, 2020).

Regarding the cross-modal interaction of visual and auditory modalities, previous work showed that increased visual perception reduces the detectability of an irrelevant auditory stimulus, causing, in this case, inattentional deafness (Macdonald & Lavie, 2011; Raveh & Lavie 2015). In support of inattentional deafness due to higher visual perceptual load, a recent review of EEG data, showed that cross-modal influences are reflected by synchronisations of ongoing neural oscillations (Bauer et al., 2020). As for VSTM load effects on auditory processing, previous work reported that neural markers indicate that VSTM load can modulate the activity of the auditory cortex (Valtonen et al., 2003). On the contrary, a recent fMRI study, found no differences in BOLD activity on the SVC or the sensory auditory cortex, when presenting auditory or visual input respectively (Gau et al., 2020). However, evidence for the cross-modal effects of VSTM load on auditory perceptual input remains sparce. Similarly, due to limited evidence, it is also still unclear if similar shared mechanisms between perception and memory exist within the auditory modality.

5.1.1 Objective

Based on numerous previous findings that VSTM load effects are sensory specific and thus impair perception, and because of the limited research on the cross-modal and auditory modality-specific effects of memory load, the aim this chapter was threefold. Firstly, I wanted to replicate previous VSTM load effects and extend them to provide evidence of impaired visual perception for irrelevant stimuli presented within the focus attention (i.e., at fixation; c.f., in periphery Konstantinou et al., 2010, 2012, 2014; Konstantinou & Lavie, 2013, 2020). Secondly, I aimed to examine the cross-modal effects of VSTM load on auditory processing, to study whether the effects of load are sensory specific or attention dependant. Lastly, my third aim was to explore whether similar effects of reduced auditory perception due to increased sensory specific load during an auditory short-term memory (ASTM) task were evident.

To explore the three aims of this chapter I conducted four new experiments. Firstly, I conducted an experiment (Experiment 3), where I hypothesized that, aligned with past findings, higher VSTM load will result in reduced visual perception. In two following experiments (Experiment 4 & 5) I focused on the cross-modal effects of VSTM load on auditory perception. According to the sensory recruitment framework, I hypothesized that auditory perception will not be affected by VSTM load manipulations, given that sensory recruitment predicts shared resources within the same modality (Pasternak & Greenlee, 2005; Lorenc & Sreenivasan, 2021; Teng & Postle, 2021). Finally, in the last experiment (Experiment 6) I adjusted the VSTM task into an ASTM task, in an effort to explore the effects of auditory load. I hypothesized that similar to the VSTM task, high ASTM load will decrease the perception of an irrelevant auditory stimulus. Below, I present the details and the results of each experiment, starting with the combined VSTM and visual-detection task.

5.2 Experiment 3: Visual Short-Term Memory Load Effects on Visual Perception

Here, I describe a combined delayed change-detection VSTM task with a visual-detection task. This combined task, was designed to replicate previous findings of impaired visual perception due to VSTM load (Lavie et al., 2014; Konstantinou et al., 2010, 2012, 2014; Konstantinou & Lavie, 2013, 2020) and further explore whether these findings expand for stimuli presented at fixation, compared to the periphery, as was the case in the previous studies.

5.2.1 Methods

5.2.1.1 Participants

Nineteen neurologically healthy adults (11 female), recruited from the Cyprus University of Technology participated in the experiment. The age of these individuals ranged between 20-42 years (*mean* = 26.1, *sd* = 6.03). Participants were screened for color deficiencies using the 10-item screening edition Ishihara Colour Deficiency Test

(Ishihara, 1987) and reported normal (or corrected to normal) colored eyesight and hearing.

5.2.1.2 Apparatus and Stimuli

The experimental procedure was designed using Psychopy3 (Pierce et al., 2019) and was run on a HP PRODESK computer. Stimuli were presented on a 21.5” Philips 226V^{la} monitor with a 60 Hz refresh rate. The monitor was placed approximately 57 cm away from the participants, whose heads were rested on a chinrest. For the VSTM task, stimuli were .6° by .6° colored squares chosen at random from nine possible colors (black, blue, cyan, green, magenta, pink, red, white, yellow). The squares were randomly presented in any one of nine positions inside an imaginary 1.8° by 1.8° square at the center of the screen with at least .3° distance in between them. For the visual-detection task, a dark grey (RGB: .66, .66, .66) circle with a radius of .5° was used. The opacity of the circle was adjusted for each participant based on an individual threshold determined using a staircase method at the beginning of the experimental procedure.

5.2.1.3 Procedure

The experimental paradigm, shown in Figure 5.1, combined a VSTM task with a visual-detection task. In detail, the procedure begun with a 100 ms black fixation dot at the center of the screen, followed by a 200 ms memory array. The memory array was either one (low load) or four (high load) colored squares, that had to be remembered. In the case of one square, only the color was to be maintained in memory. When four squares were presented both the color and the position had to be held in memory. Low and high load conditions were presented in a counterbalanced blocked design (ABBABAAB) within eight blocks (four low and four high). After the memory probe disappeared, a 3000 ms memory retention period followed. During this memory retention period, a black fixation dot was present at the center of the screen. In 50% of the trials, 1000 ms after the maintenance period begun, the detection stimulus was presented for 100 ms - within the focus of attention- at fixation. At 1100 ms, the phrase “*Seen?*” appeared 1.4° above fixation, indicating to the participants to respond, using the “A” and “S” keys of the keyboard, whether the dark grey circle was present or absent (“A” = absent, “S” = present). The phrase “*Seen?*” disappeared as soon as a response was given, and the black fixation dot remained on screen until the 3000 ms maintenance period was over.

Figure 5. 1: Trial procedure in the combined VSTM and visual-detection task.

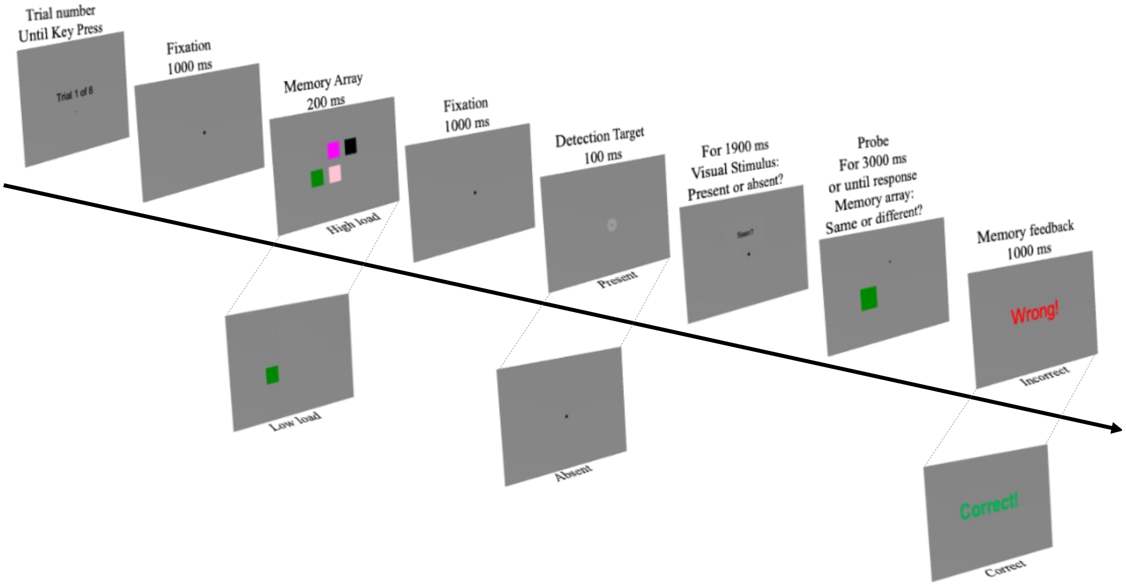


Fig.5.1. Each trial begins with a screen indicating the trial number. A key press (spacebar) is required for the trial to proceed. Following the key press a 1000 ms fixation dot is presented followed by a 200 ms memory array. In the low load conditions (50% of all trials) one colored square is presented, whereas in the high load condition (50% of all trials) four squares are presented. During a 3000 ms delay period (maintenance/retention phase) a visual stimulus consisting of a dark grey circle with an individually determined opacity is presented at 1000 ms in 50% of the trials for 100 ms. At 1100 ms during the retention period a text probe (‘Seen?’) indicates to the participants to respond whether the visual stimulus was present or absent. After the 3000 ms retention period, a memory probe, consisting of one square, appears where participants have up to 3000 ms to respond whether it is the same or different than any one square of the memory array. Feedback is provided, only for the memory task, for 1000 ms after the response to the memory probe by the word ‘Wrong!’ in red letters (incorrect memory trials) or the word ‘Correct!’ in green letters (correct memory trials).

Next, a probe consisting of one colored square appeared, where participants had to indicate whether it was the same or different than any one square that was held in memory, using the arrow keys (Left Arrow Key = same, Down Arrow Key = different). In the low load condition, in 50% of the trials the memory probe had a different color than the remembered one, chosen at random from the remaining seven color choices. In the high load condition, in 50% of the trials the memory probe was different as follows: in half of the different trials (25% of total trials) the memory probe had a different color chosen from the remaining five color choices, and in the rest half of the different trilas (25% of total trials) the memory probe had the color of one of the squares from the memory array, but presented at a different position. The probe was present for 3000 ms, or until a response was given. After each trial, feedback was provided for 1000 ms for the VSTM task only, with the word “*Correct*” presented in green letters for correct VSTM trials, or the word “*Wrong*” presented in red letters for incorrect VSTM trials.

The participants were instructed to respond to both tasks as quickly and as accurately as possible, without sacrificing accuracy for speed. Each one of the eight blocks contained 48 trials (384 total trials).

5.2.1.4 Data Analysis

As in Chapter 4, analyses were conducted using Jamovi (The Jamovi Project, 2022, Version 2.3.13; https://www.jamovi.org), using a Bayesian framework.

To estimate VSTM capacity in each load condition I computed Cowan's *K* (Cowan et al., 2015):

$$\mathrm{K} = \mathrm{N}\,(\mathrm{H} - \mathrm{FA})$$

where K is the memory estimate calculated by multiplying the difference between Hits (H) and False Alarms (FA), in the VSTM task, by the number of items presented in the memory sample (N). To establish the successful manipulation of VSTM load, a Bayesian paired *t*-test was computed between low load and high load *K*, using a Cauchy prior with a width $r = .93$, according to the results of previous studies (Konstantinou & Lavie, 2013; Konstantinou et al., 2014). Similarly, accuracy rates between low load and high load were compared using a Bayesian paired *t*-test, using a Cauchy prior with a width $r = 1.91$, derived from a previous, similar study (Konstantinou & Lavie, 2013; Konstantinou et al., 2014).

To test my main hypothesis that VSTM load will impair visual detection, I conducted a Bayesian paired *t*-test for the difference in the visual-detection task detection sensitivity (*d'*) between the low load and high load VSTM conditions. The Cauchy prior for this analyses was set to $r = 0.6$, according to previous findings (Konstantinou & Lavie, 2013; Konstantinou et al., 2014). To ensure that the effects were indeed due to VSTM load and to control for other confounders, *d*' measurements were taken only from correct VSTM task trials. Additionally, the slowest and fastest responses of each participant were removed from the analyses, by excluding any data that concerned response times that were further than 3 *sd*s away from each participant's mean reaction time. Accuracy rate differences between the low and high load conditions were analysed using a Bayesian paired *t*-test with a Cauchy prior width set to $r = 1.49$, based on previous studies (Konstantinou & Lavie, 2013; Konstantinou et al., 2014).

5.2.2 Results

The overall mean accuracy rate in the VSTM task was 88% (*sd* = 8%), with higher accuracy in the low load (mean = 96%, *sd* = 4%) compared to the high load (mean = 80%, *sd* = 12%) condition (BF_{10} = 36565). Load manipulation was successful as indicated by the comparisons between low load (K = .91 *sd* = .08) and high load (K = 2.36 *sd* = .99) Cowan's K capacity estimates (BF_{10} = 9427). Based on reaction time filtering 2.75% (*sd* = 3.19%) of trials were excluded, on average. For the visual detection task, comparisons between the mean accuracy rates provided evidence of differences between accuracy in the low load (mean = 91%, *sd* = 11%) and high load (mean = 88%, *sd* = 14%) condition (BF_{10} = 8.52). Regarding the main hypothesis of this experiment, evidence was found in favor of a difference for d' between the low load (d' = 3.26, *sd* = 1.08) and high load (d' = 2.87, *sd* = 1.12) condition (BF_{10} = 4.92). The rainplot of d' in the visual-detection task for the low load and high load condition is shown in Figure 5.2. These results replicate the effects of VSTM load on visual perception found in previous work (Lavie et al., 2014; Konstantinou et al., 2010, 2012, 2014; Konstantinou & Lavie, 2013, 2020) and indicate that higher VSTM load can impair the detection of an irrelevant stimulus, even if that stimulus is presented within the focus of attention, at fixation. This effect is in agreement with my hypothesis, and the predictions of the sensory recruitment framework. Next, I explore the cross-modal effects of VSTM load, by switching the detection task from visual to auditory.

Figure 5. 2: Results for Experiment 3 with 19 participants.

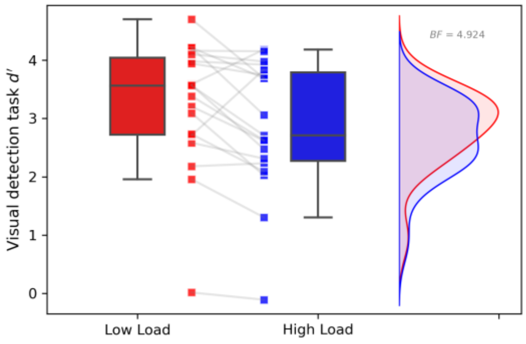


Fig.5.2. Mean and individual detection sensitivity (d') in the visual-detection task of Experiment 3 for the low VSTM load (red) and high VSTM load (blue) conditions.

Notes. VSTM; visual short-term memory.

5.3 Experiment 4: Visual Short-Term Memory Load Effects on Auditory Perception

Despite the sensory specific effects of VSTM load, it still remains questionable whether these effects are modality specific or can be observed cross-modally. To address this question, here, I replaced the visual-detection task with an equivalent auditory-detection task.

5.3.1 Methods

5.3.1.1 Participants

Thirty-five new participants (26 female) were recruited from the Cyprus University of Technology. Participants' age ranged between 19-57 years (*mean* = 25.8, *sd* = 7.53). No color deficiencies were found according to the 10-item screening edition Ishihara Colour Deficiency Test (Ishihara, 1987) and participants reported normal (or corrected to normal) eyesight and hearing.

5.3.1.2 Apparatus and Stimuli

The apparatus and stimuli used in this experiment were identical to those used in Experiment 3 (see *5.2.1.2 Apparatus and Stimuli*). For the audio-detection task (which replaced the visual-detection task of the previous experiment) a 1000 Hz pure tone was presented in stereo through a set of Bose QuietComfort 35 wireless headphones II. The volume of the auditory stimulus was adjusted for each participant based on an individual threshold determined using a staircase method at the beginning of the experimental procedure.

5.3.1.3 Procedure

The procedure followed in Experiment 4 was similar to Experiment 3 (see *5.2.1.3 Procedure*) and is illustrated in Figure 5.3. There were two differences from the previous experiment. Specifically, the first difference was that the visual-detection task was replaced with an auditory-detection task, where, instead of the visual stimulus, in 50% of the trials, 1000 ms after the maintenance period begun, the auditory stimulus was presented for 100 ms. The second difference was that the phrase "*Seen?*" was replaced with a change of the fixation dot, to motivate participation. In detail, at 1100 ms, the fixation dot changed to white, indicating to the participants to respond to the detection task, as previously. As in Experiment 3, participants completed eight counterbalanced blocks (ABBABAAB), which contained 48 trials each (384 total trials).

Figure 5. 3: Trial procedure in the combined VSTM and auditory-detection task.

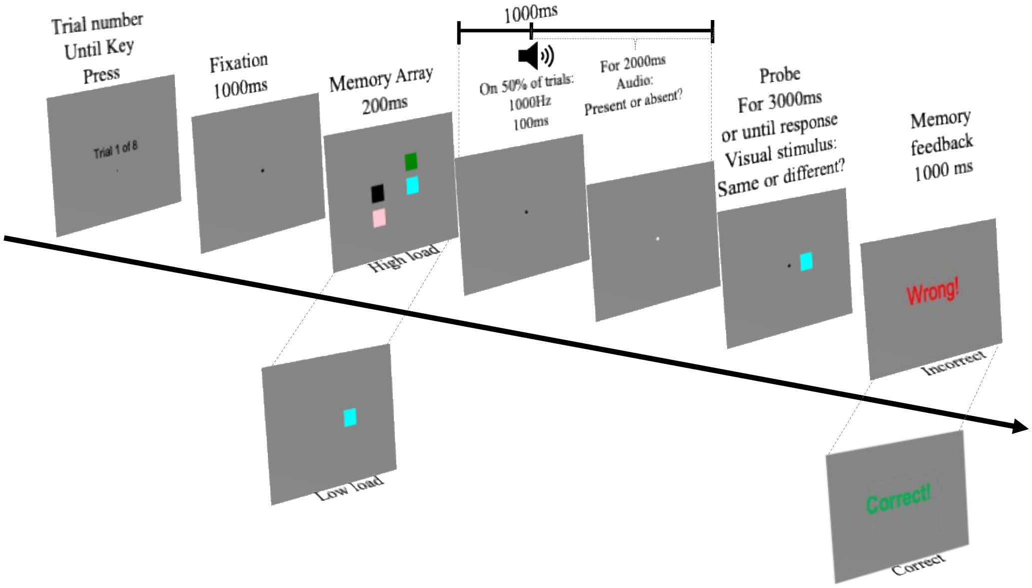


Fig.5.1. Each trial begins with a screen indicating the trial number. A key press (spacebar) is required for the trial to proceed. Following the key press a 1000 ms fixation dot is presented followed by a 200 ms memory array. In the low load conditions (50% of all trials) one colored square is presented, whereas in the high load condition (50% of all trials) four squares are presented. During a 3000 ms delay period (maintenance/retention phase) an auditory stimulus consisting of a pure 1000 Hz tone with an individually determined volume is presented at 1000 ms in 50% of the trials for 30 ms. At 1100 ms during the retention period the fixation dot turns white, indicating to the participants to respond whether the auditory stimulus was present or absent. After the 3000 ms retention period, a memory probe, consisting of one square, appears where participants have up to 3000 ms to respond whether it is the same or different than any one square of the memory array. Feedback is provided, only for the memory task, for 1000 ms after the response to the memory probe by the word 'Wrong!' in red letters (incorrect memory trials) or the word 'Correct!' in green letters (correct memory trials).

5.3.1.4 Data Analysis

Data analysis was identical to Experiment 3 (see *5.2.1.4 Data Analysis*). To test the main hypothesis for Experiment 4 that VSTM load will not impair auditory detection, a Bayesian paired *t*-test was conducted, testing the difference in the auditory-detection task detection sensitivity (*d'*) between the low load and high load VSTM conditions. As described in Chapter 4 (see *4.2.1.5 Analysis Plan*), a main advantage of implementing a Bayesian analysis, is that contrary to the *p*-value, which can only provide information about the rejection of the null hypothesis (Johansson, 2011), a *BF* can quantify evidence in favor of either the alternative or the null hypotheses (Dienes, 2014; Dienes & Mclatchie, 2018; van Ravenzwaaij, & Etz, 2021; Wagenmakers, 2007). Hence, this characteristic of the *BF* allows me to hypothesize in favor of no difference between low load and high load *d’* for Experiment 4.

5.3.2 Results

The overall mean accuracy rate in the VSTM task was 85% (*sd* = 8%). Higher accuracy rates were found in the low load (mean = 95%, *sd* = 5%) in comparison with the high load (mean = 75%, *sd* = 11%) condition ($BF_{10} = 9.52 \text{ x } 10^{11}$). The comparisons between low load (*K* = .9 *sd* = .1) and high load (*K* = 2.02 *sd* = .92) Cowan’s *K* capacity estimates provided evidence that load manipulation was successful ($BF_{10} = 2.67 \text{ x } 10^{6}$). On average, 3.58% (*sd* = 4.69%) of trials were excluded based on reaction time filtering. Accuracy rates for the auditory detection task were similar between the low load (mean = 86%, *sd* = 18%) and high load (mean = 88%, *sd* = 13%) conditions as reflected by evidence in favor of a null hypothesis ($BF_{10} = .12$), a finding that supports no accuracy differences between the two conditions. Regarding the main hypothesis of this experiment, evidence was in support of the alternative hypothesis of no difference for *d’* between the low load (*d’* = 2.9, *sd* = 1.48) and high load (*d’* = 2.81, *sd* = 1.49) condition ($BF_{10} = .29$). Figure 5.4 presents the rainplot of auditory-detection *d’* for the low load and high load condition. To the best of my knowledge, there is no evidence for the cross-modal effects of VSTM load on auditory perception, however, my findings contradict those of previous work on perceptual load that showed inattentional deafness that was attributed to the increased sensory demands of the visual modality (Macdonald & Lavie, 2011; Raveh & Lavie 2015). The absence of a cross-modal effect is aligned with my hypothesis and with the sensory recruitment framework, since the foundation of sensory recruitment is the selective processing of specific visual features of SVC neurons (Harrison & Tong, 2009; Issa et al., 2008; Konstantinou et al., 2012; Serences et al., 2009). However, it is possible that the failure to induce inattentional deafness, was due to the features of the auditory-detection task, which possibly made the task very easy, as reflected by the high detection sensitivity index in both low and high load conditions (*d’* > 2.8). To rule out this possibility I adjusted the combined VSTM and auditory-detection task, to increase its difficulty, as I present next.

Figure 5. 4: Results for Experiment 4 with 35 participants.

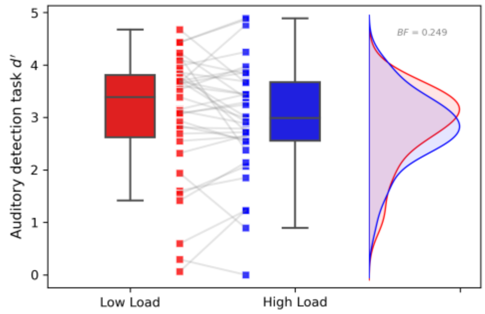


Fig.5.4. Mean and individual detection sensitivity (*d'*) in the auditory-detection task of Experiment 4 for the low VSTM load (red) and high VSTM load (blue) conditions.

Notes. VSTM; visual short-term memory.

5.4 Experiment 5: Visual Short-Term Memory Load Effects on Auditory Perception – Adapted Detection Task

Experiment 4 indicated that, as per the predictions of the sensory recruitment framework, no cross-modal effects were evident in the combined VSTM and auditory-detection task. Though, the evidence in favor of no difference (i.e., no inattentional deafness) could be due to the design of the auditory-detection task, which made the task easy. In Experiment 4, the auditory-detection task was designed to match the visual-detection task of Experiment 3. Therefore, the auditory stimulus was presented for 100 ms. However, the processing of visual and auditory stimuli has been shown to differ (Jose & Kumar, 2010), and it is suggested that 100 ms is a long enough duration to guarantee the perception of a pure tone (Garner & Miller, 1947; Jeon & Fricke, 1997; Näätänen & Winkler, 1999; Tekman, 1997). In Experiment 5, I therefore adjusted the auditory-detection task to account for the long duration of the pure tone that was used previously. An additional adjustment that was made to increase the difficulty of Experiment 5, was the introduction of a jitter to the initiation of the auditory-detection task. The jitter has been introduced since temporal expectations during VSTM task have been shown to improve performance (Gresch et al., 2021; Loyola-Navarro et al., 2022; Turatto & De Tommaso, 2022).

5.4.1 Methods

5.4.1.1 Participants

For Experiment 5 I recruited 28 new participants (22 female) from the Cyprus University of Technology, whose age ranged between 18-42 years (*mean* = 23.8, *sd* =

5). According to the 10-item screening edition Ishihara Colour Deficiency Test (Ishihara, 1987) no color deficiencies were found and participants reported normal (or corrected to normal) eyesight and hearing.

5.4.1.2 Apparatus and Stimuli

The apparatus and stimuli used in Experiment 5 were identical to those used in Experiment 4 (see *5.3.1.2 Apparatus and Stimuli*).

5.4.1.3 Procedure

The procedure followed here was almost identical to that of Experiment 4 (see *5.3.1.3 Procedure*; see also Figure 5.3). There were two differences in Experiment 5. The first difference was that the auditory-detection stimulus was now presented for 30 ms instead of 100 ms, so that its perception becomes more difficult. The second difference was that the auditory-detection task was now presented randomly, but in a counterbalanced manner in each block, either at 800 ms (50% of trials) or at 1200 ms (50% of trials) after the onset of the memory delay, to reduce temporal expectations. As with the previous experiments presented in this Chapter, Experiment 5 consisted of eight counterbalanced blocks (ABBABAAB) with 48 trials in each (384 total trials).

5.4.1.4 Data Analysis

Data analysis was the same as in Experiment 4 (see *5.3.1.4 Data Analysis*). A Bayesian paired *t*-test was implemented, which tested the difference in the auditory-detection task detection sensitivity (*d'*) between the low load and high load VSTM conditions, to test the main hypothesis of Experiment 5 that VSTM load will not impair auditory detection.

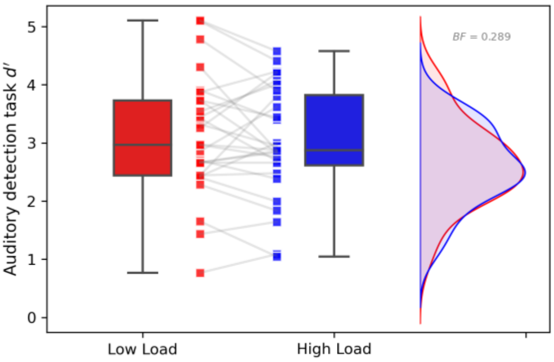
5.4.2 Results

Participants in Experiment 5 had an overall mean accuracy rate of 85% (*sd* = 7%) in the VSTM task. Accuracy rates in the low load (mean = 95%, *sd* = 4%) were higher compared to the high load (mean = 75%, *sd* = 11%) condition ($BF_{10} = 1.24 \times 10^{10}$). As before, load manipulation was deemed successful, as reflected by the comparisons between low load (*K* = .9 *sd* = .09) and high load (*K* = 2.04 *sd* = .88) Cowan's *K* capacity estimates (BF_{10} = 240243). Following reaction time filtering, 3.52% (*sd* = 6.71%) of trials, on average, were excluded. In the auditory detection task, accuracy rates similar between the low load (mean = 90%, *sd* = 8%) and high load (mean = 89%, *sd* = 9%) conditions as reflected by evidence favoring the null hypothesis (BF_{10} = .15). For the main hypothesis of Experiment 5, evidence was in favor of the alternative hypothesis, indicating no difference in *d'* between the low load (*d'* = 3.1, *sd* = 1.02) and high load (*d'* = 3.02, *sd* = .95) condition (BF_{10} = .29). The rainplot of auditory-detection *d'* for the low load and high load condition in Experiment 5 is shown in Figure 5.5. These results resonate the findings of Experiment 4, and are in harmony with my hypothesis and, subsequently, with the sensory recruitment framework. Particularly, a hallmark of the sensory recruitment framework is the common neural processing of sensory-specific features between perception and short-term memory (Pasternak & Greenlee, 2005; see also Lorenc et al., 2021). As shown by the results of Experiments 4 and 5, given the selectivity of the SVC for processing elemental visual features, it is likely that no interferences would be found cross-modally, since WM demands remain within sensory-specific capacity (Harrison & Tong, 2009; Rademaker et al., 2019; Serences et al., 2009; Supèr et al., 2001; for reviews see Lorenc et al., 2021; Pasternak & Greenlee, 2005; Postle, 2006, 2015, 2016; Serences, 2016; Teng & Postle, 2021). A remaining question is whether similar perceptual impairments due to memory load can be found for the auditory modality. I explore this with the next experiment.

Figure 5. 5: Results for Experiment 5 with 28 participants.

Fig.5.5. Mean and individual detection sensitivity (*d'*) in the auditory-detection task of Experiment 5 for the low VSTM load (red) and high VSTM load (blue) conditions.

Notes. VSTM; visual short-term memory.



5.5 Experiment 6: Auditory Short-Term Memory Load Effects on Auditory Perception

Because of the increased difficulty to design and implement an equivalent VSTM delayed match-to-sample or change-detection task in the auditory modality, sensory recruitment research has remained focused in the visual system (Adam et al., 2021; Teng & Postle, 2021; see also Shevlin, 2020). Here, I adjusted the VSTM task used in Experiments 3, 4, and 5, in an effort to conduct a comparable ASTM task and consequently manipulate auditory load. With this adjustment, I attempted to explore whether there is evidence for a similar shared mechanism between perception and memory within the auditory system.

5.5.1 Methods

5.5.1.1 Participants

I recruited 24 new participants (17 female) from the Cyprus University of Technology, who took part in Experiment 6 and whose age ranged between 18-35 years (*mean* = 25.5, *sd* = 4.22). Participants reported normal (or corrected to normal) eyesight and hearing.

5.5.1.2 Apparatus and Stimuli

The apparatus and the stimuli for the auditory-detection task used in Experiment 6 was the same as in Experiment 5. For the ASTM task, stimuli consisted of pure tones chosen at random from nine possible frequencies (750 Hz, 800 Hz, 850 Hz, 900 Hz, 950 Hz, 1000 Hz, 1050 Hz, 1100 Hz, 1150 Hz).

5.5.1.3 Procedure

Here, the experimental paradigm, presented in Figure 5.6, combined an ASTM task with the auditory-detection task used in Experiment 5. Regarding the procedure of the ASTM task, it begun with a 100 ms black fixation dot at the center of the screen. This was followed by a sequential auditory memory array that was designed to match the timing of the VSTM memory array presentation of the previous experiments. In detail, two pure tones were presented sequentially for 50 ms each, with a 100 ms blank delay in between, at a volume set to 300% of the identified threshold from the auditory-detection

Figure 5. 6: Trial procedure in the combined ASTM and auditory-detection task.

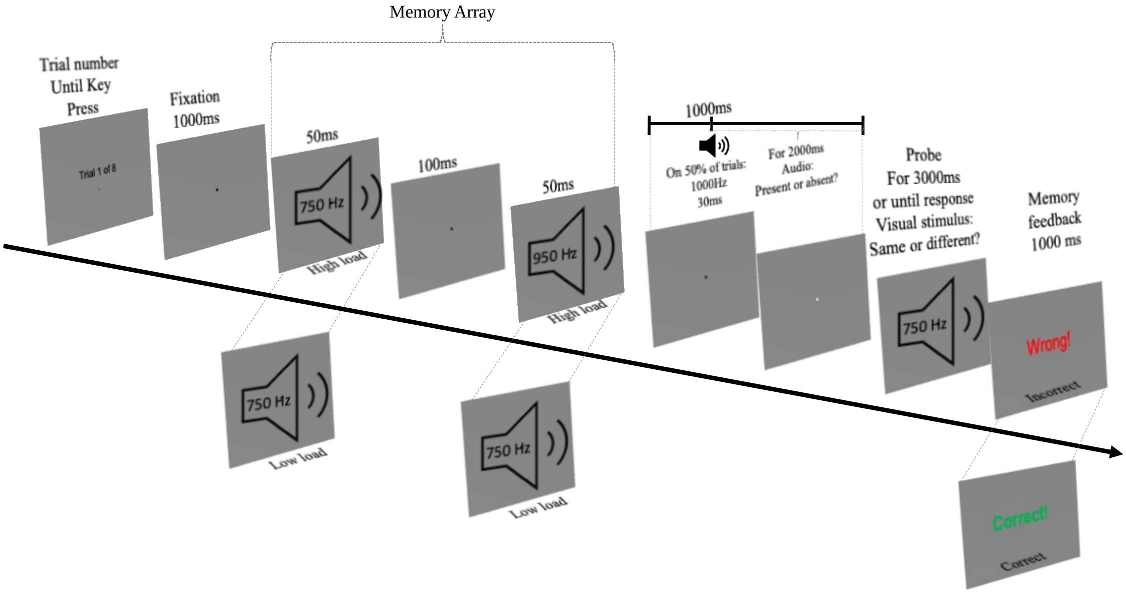


Fig.5.6. Each trial begins with a screen indicating the trial number. A key press (spacebar) is required for the trial to proceed. Following the key press a 1000 ms fixation dot is presented followed by a 200 ms memory array. In the low load conditions (50% of all trials) one pure tone is presented twice, whereas in the high load condition (50% of all trials) two tones are presented, only once each. During a 3000 ms delay period (maintenance/retention phase) an auditory stimulus consisting of a pure 1000 Hz tone with an individually determined volume is presented at 1000 ms in 50% of the trials for 30 ms. At 1100 ms during the retention period the fixation dot turns white, indicating to the participants to respond whether the auditory stimulus was present or absent. After the 3000 ms retention period, a memory probe, consisting of one tone is heard and participants have up to 3000 ms to respond whether it is the same or different than any one square of the memory array. Feedback is provided, only for the memory task, for 1000 ms after the response to the memory probe by the word ‘Wrong!’ in red letters (incorrect memory trials) or the word ‘Correct!’ in green letters (correct memory trials).

task for each participant. In the low load condition, the two pure tones were of the exact same frequency, meaning that participants had to remember only one tone, which they had heard twice. In the high load condition, the two tones were different by at least 200 Hz, and participants had to remember both, which they had heard only once each. Contrary to the VSTM load experiments, only two memory items were used in the ASTM task to counterweigh for the increased difficulty of the task. After the 3000 ms memory retention period, where the auditory-detection task took place as previously, a probe consisting of a single 50 ms pure tone was played. Participants had to indicate whether it was the same or different than any of the tones from the memory array. In 50% of the trials, the tone was different by 150 Hz for either the first or the second tone of the memory array. The direction of the difference (above or below), as well as the probed memory array stimulus (first or second) was counterbalanced across all blocks. After listening to the memory probe, participants had up to 3000 ms to respond to the ASTM task. In total, Experiment 6 comprised of eight counterbalanced blocks (ABBABAAB) with 48 trials in each (384 total trials).

5.5.1.4 Data Analysis

The same data analysis approach as in Experiment 5 was used (see *5.4.1.4 Data Analysis*). I used a Bayesian paired *t*-test, which tested the difference in the auditory-detection task detection sensitivity (*d’*) between the two ASTM conditions, low load and high load, to test the main hypothesis of Experiment 6 that increased ASTM load will impair auditory detection.

5.5.2 Results

The overall mean accuracy rate in the ASTM task was 80% (*sd* = 11%). Higher accuracy rates were found for the low load (mean = 82%, *sd* = 12%) compared to the high load (mean = 77%, *sd* = 11%) condition (BF_{10} = 82.4). Similarly to the previous VSTM experiments, ASTM load manipulation was successful, as supported by the Cowan’s *K* capacity estimate comparisons between the low load (*K* = .64 *sd* = .24) and high load (*K* = 1.09 *sd* = .45) conditions (BF_{10} = 536990). Filtering according to reaction times, resulted in the exclusion of 4.22% (*sd* = 5.91%) of trials, on average. Accuracy rates in the auditory detection task showed no differences between the low load (mean = 85%, *sd* = 14%) and high load (mean = 84%, *sd* = 14%) conditions (BF_{10} = 011). Evidence for the main hypothesis of Experiment 6, supported the alternative hypothesis, of no difference in *d’* between the low load (*d’* = 2.68, *sd* = 1.21) and high load (*d’* = 2.65, *sd* = 1.20) condition (BF_{10} = .26). The results of the comparison for auditory-detection *d’* in the low load and high load ASTM condition in Experiment 6 are illustrated as a rainplot in Figure 5.7. The findings of Experiment 6 oppose my hypothesis, and contrary to the predictions of sensory recruitment, no effects on auditory perception were found after taxing auditory memory. A possible explanation of this finding is likely attributed to the notion that the nature of the ASTM system differs from VSTM. This is supported by vast research showing the robustness of auditory perception to various distractors and cognitive demands (Dalton, & Lavie, 2004; Escera et al., 2002, 2003; Kim et al., 2022; Mandal et al., 2022; Tellinghuisen & Nowak, 2003). Even though evidence in favor of no effects on auditory detection were found either due to ASTM (Experiment 6) nor due to VSTM (Experiments 4 and 5) load, it is possible that this finding is attributed to other factors, such as task difficulty. To investigate this, I next turn to a comparison of the four studies conducted in Chapter 5.

Figure 5. 7: Results for Experiment 6 with 24 participants.

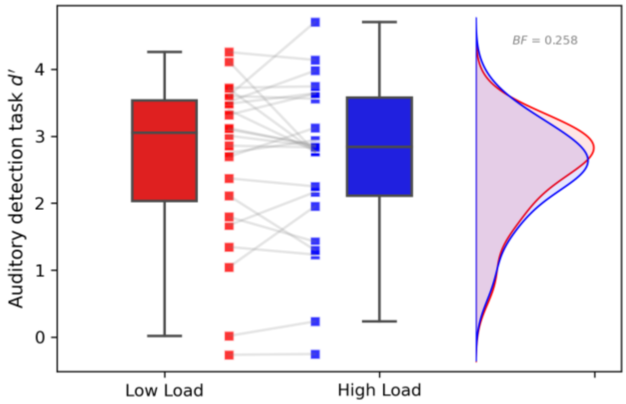


Fig.5.7. Mean and individual detection sensitivity (*d'*) in the auditory-detection task of Experiment 6 for the low ASTM load (red) and high ASTM load (blue) conditions.

Notes. ASTM; auditory short-term memory.

5.6 Comparison of Effects in Experiments 3, 4, 5, and 6

My findings thus far show that higher VSTM load impairs visual detection as compared to low VSTM load, however, for cross-modal VSTM and auditory detection effects (Experiments 4 and 5), as well as for ASTM and auditory detection effects (Experiment 6), the evidence favored no difference between low and high load conditions. Taken together, these findings can be attributed to a shared mechanism between memory and perception in the visual domain (Lavie et al., 2014; Konstantinou et al., 2010, 2012, 2014; Konstantinou & Lavie, 2013, 2020), as proposed by the sensory recruitment framework (see Pasternak & Greenlee, 2005; Lorenc et al., 2021). However, an alternative explanation of the findings presented here may be attributed to task difficulty. In detail, one argument against memory load effects is that detection impairments might not be due to load effects per se, but due to a general increase in task difficulty (see Konstantinou et al., 2014; Konstantinou & Lavie, 2013, 2020; Lavie & De Fockert, 2003). Greater difficulty in a given task might result in an increase in the demand of general cognitive capacity resources (e.g., Fougnie & Marois, 2007; for a review see Murphy et al., 2016) instead of sensory specific resources as claimed in this thesis. For example, Tsal and Benoni (2010) argue that perceptual load effects can be explained by greater non-specific demands on some general cognitive resource, through dilution. Dilution suggests that distractor effects disappear under high load, not due to increased perceptual demands, but because the distractor interference weakens in the presence of additional stimuli (Tsal, & Benoni, 2010; see also De Fockert, 2013). As such, here, the impaired visual detection found in Experiment 3, might in fact be due to the increased difficulty of the VSTM and/or the visual detection task, instead of a competition between perceptual and memory processes. Along the same lines, the evidence in favour of no-load effects found in Experiments 4, 5, and 6, might be due to the level of difficulty of the memory and/or the detection tasks, which in turn limit the exploration of any load differences. To investigate the effects of task difficulty, for both the memory and detection tasks, I compared the performance of participants across the four experiments presented in this chapter.

5.6.1 Data Analysis

To analyse performance differences across the four experiments I conducted two Bayesian rmANOVAs. Task difficulty was assessed by setting mean accuracy rates as the depended variable of the rmANOVA, separately for the low load and high load conditions. As such, one rmANOVA was conducted on the mean accuracy rates of the memory task (VSTM in Experiments 3, 4, 5, and ASTM in Experiment 6), and a second rmANOVA was conducted on the mean accuracy rates of the detection task (visual in Experiment 3, auditory in Experiments 4, 5, 6). The experiment by which data were collected was set as a between group factor. This procedure resulted in a two (Load: low vs. high) by four (Experiment: 3 vs. 4 vs. 5 vs. 6) design for each of the two rmANOVAs. The rmANOVAs were informed using the priors suggested by Rouder et al. (2012) that assume Cauchy distributions centered on 0 (fixed effects r = .5; random effects r = 1). For the post-hoc t-tests that followed, I used a Cauchy distribution centered on 0 with a width set to 0.707, as proposed by Rouder et al. (2009).

5.6.2 Results

The mean accuracy rates for the memory and detection tasks are summarized in Table 5.1 for each experiment, separately for the low and high load conditions.

Table 5. 1: Mean Accuracy Rates for Experiments 3, 4, 5, and 6 for the memory and the detection tasks.

	Memory Task Accuracy (*sd*)		**Detection Task Accuracy (*sd*)**	
Experiment	**Low Load**	**High Load**	**Low Load**	**High Load**
3	96% (4)	80% (12)	91% (11)	88% (14)
4	95% (5)	75% (12)	89% (13)	88% (13)
5	95% (4)	75% (11)	90% (9)	89% (8)
6	82% (11)	77% (11)	85% (14)	84% (14)

5.6.2.1 Memory Task Difficulty Comparison

The results from the rmANOVA (Figure 5.8) on the accuracy rates of the memory task indicated evidence in favor of effects due to the load factor ($BF_{incl} = 1.14 \times 10^{14}$), the experiment factor ($BF_{incl} = 1.12 \times 10^{7}$), and the interaction of these two factors ($BF_{incl} = 1.85 \times 10^{7}$). Given the successful load manipulation previously reported in each of the four experiments, evidence in favor of the load factor was expected. The exploration of the evidence in favor of the experiment factor, through post-hoc analyses, revealed that this effect derives from differences between Experiment 6 with Experiments 3 ($BF_{10} = 10.84$), 4 ($BF_{10} = 2.05$), and 5 ($BF_{10} = 1.9$), with these differences being at least twice as likely, as reflected by the *BF*. Additionally, evidence of no differences between Experiments 4, 5, and 6 was found (all $BFs_{10} < .32$). A deeper investigation of the interaction effect, showed that the interaction is driven by the reduced accuracy rates found in the low load condition of Experiment 6, as compared to Experiment 3 ($BF_{10} = 714.78$), 4 ($BF_{10} = 34381.02$), and 5 ($BF_{10} = 5857.41$). Evidence of no such difference, by a two-fold factor, across all experiments was found for the high load condition (all $BFs_{10} < .54$). Overall, these results reveal that, for the memory task, the low load condition of Experiment 6 was more difficult compared to the rest of the experiments, showcasing a difference between the VSTM and ASTM tasks. For the high load condition of the memory task, the difficulty was the same across all experiments. Along these lines, Experiments 3, 4, and 5, which all used the same VSTM task, showed no differences regarding task difficulty.

Figure 5. 8: Mean Accuracy Rates for Experiments 3, 4, 5, and 6 in the memory task.

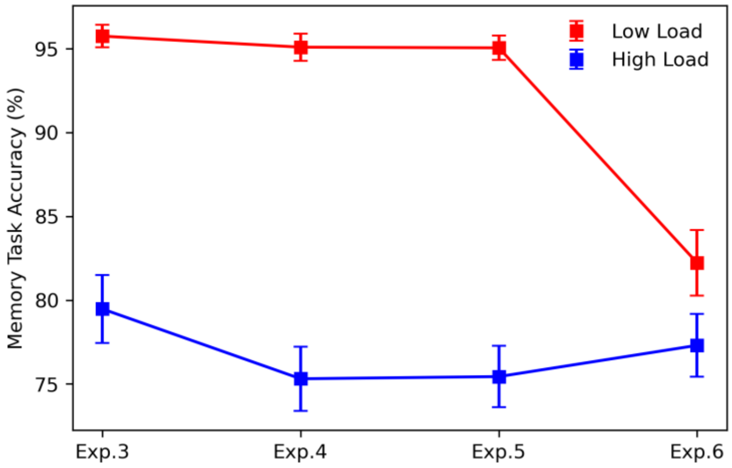


Fig.5.8. Mean accuracy rates in the memory task across Experiments 3, 4, 5, and 6 for the low load (red) and high load (blue) conditions.

Notes. Exp; experiment.

5.6.2.2 Detection Task Difficulty Comparison

For the detection task accuracy rates, the results from the rmANOVA (Figure 5.9) resulted in inconclusive evidence regarding the load factor (BF_{incl} = .88), but there was evidence against an effect by the experiment factor (BF_{incl} = .42) and the interaction of the two factors (BF_{incl} = .20), by a magnitude greater than two. The inconclusive evidence concerning the load factor is most likely driven by the fact that Experiment 3 showed an effect of load on detection sensitivity (see *5.2.2 Results*), while the rest of the experiments resulted in a null effect. The evidence against the effect of the experiment factor and the interaction was not surprising, considering that the detection task difficulty was adjusted using the same staircase procedure in all experiments (see *5.2.1.2 Apparatus and Stimuli*). Considering the results of the rmANOVA for the detection task accuracy rates, it is concluded that the detection task difficulty was similar across all four experiments. Next, I turn to a summary of the results presented in this chapter.

Figure 5. 9: Mean Accuracy Rates for Experiments 3, 4, 5, and 6 in the detection task.

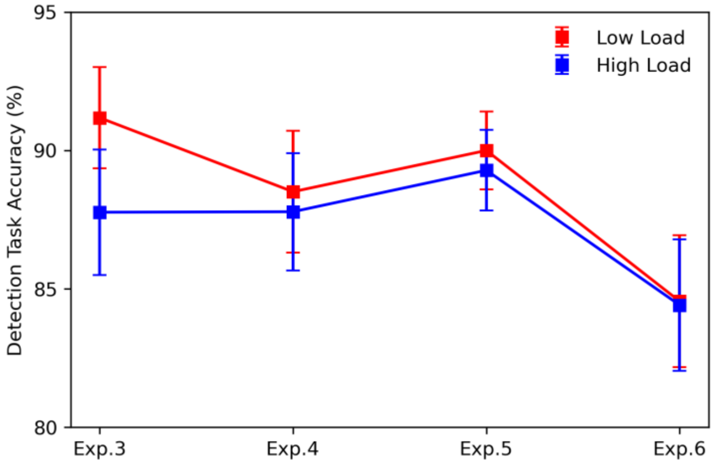


Fig.5.9. Mean accuracy rates in the detection task across Experiments 3, 4, 5, and 6 for the low load (red) and high load (blue) conditions.

Notes. Exp; experiment.

5.7 Chapter 5 Summary

The manipulation of VSTM load has been vastly used in previous studies, showing that it interferes with SVC activity and signifying a shared neural mechanism between memory and perception (Lavie et al., 2014; Konstantinou et al., 2010, 2012, 2014; Konstantinou & Lavie, 2013, 2020). In this chapter, with Experiment 3, I utilized such load manipulations and showed that the detection of an irrelevant visual stimulus, even within the focus of attention, decreases due to increased VSTM load. This replicated previous findings from the literature and further supported the idea of a shared neural resource between VSTM and visual perception, which is the foundation of the sensory recruitment framework (Pasternak & Greenlee, 2005; Lorenc et al., 2021). Moreover, to rule out the possibility that the decrease of the perception of irrelevant stimuli is due to attentional, rather than sensory, demands, I conducted two additional experiments. Experiments 4 and 5, explored the effects of VSTM load on the perception of auditory stimuli, where I showed that there was no difference on auditory detection between low and high VSTM load conditions. Finally, in an effort to investigate whether sensory recruitment generalizes to the auditory modality, I designed and conducted an ASTM task, where I manipulated auditory load. The results of this ASTM task showed that auditory load did not affect auditory perception, a finding that supports the view that the ASTM system likely differs from VSTM. However, given the increased difficulty of the low load condition in the ASTM task, this finding needs to be taken with caution, as I discuss in detail in the next section (see *6.2.3 Limitations and Alternative Explanations*). In the next and final chapter, I present a general discussion of the results of this thesis.

6 General Discussion

6.1 Discussion Overview

In this thesis I investigated the debated sensory recruitment framework of VSTM through a systematic review (Chapter 2), three meta-analyses and two meta-regressions (Chapter 3), two TMS experiments (Chapter 4), and four behavioral experiments (Chapter 5). Collectively, all evidence presented throughout Chapters 2 to 5 point towards the involvement of the SVC during the maintenance of information during VSTM. In this final chapter, I provide an overall appraisal of these findings, highlight some of the limitations of this thesis, and discuss possible future directions on the basis of my results.

6.2 The Sensory Recruitment Framework: Resolving the Debate

This thesis has provided compelling evidence for the involvement of the SVC in the brain network responsible for successful maintenance of information during VSTM. Below, I elaborate on the main findings derived from each chapter.

6.2.1 Evidence for the Sensory Recruitment Framework Through Transcranial Magnetic Stimulation

Contrary to the correlational nature of neuroimaging tools, TMS can provide causal information regarding the brain network underlying behavioral responses (Bergmann, & Hartwigsen, 2021; Pitcher et al., 2020). For this reason, the main evidence for this thesis was derived from TMS findings. Initially, a systematic review (Chapter 2) was conducted to investigate whether the SVC is part of the brain network responsible for the encoding as well as the short-term maintenance of visual information. I focused on studies that interfered with SVC using TMS during the encoding and maintenance phases of VSTM. The systematic review identified 14 papers that included 18 experiments and totaling 248 participants. This systematic review was supplemented by two meta-analyses, two meta-regressions and one exploratory meta-analysis. The meta-analyses investigated separately the role of the SVC in encoding and short-term maintenance of visual information. The meta-regressions explored whether the different stimulation timings of all included studies are related to the effect of the stimulation.

The exploratory meta-analysis investigated the direction of the stimulation effects, indicating an inhibition effect for TMS during VSTM encoding and a facilitatory effect for TMS during VSTM maintenance.

In the six experiments described in the systematic review, all but one provided significant evidence that TMS during the encoding phase of VSTM can affect memory performance (Cattaneo et al., 2009; Koivisto et al., 2017; Rademaker et al., 2017; van Lamsweerde, & Johnson, 2017). In addition, the quantitative analysis of the studies included in the meta-analysis further supports the presence of an effect of TMS on SVC during the encoding phase of VSTM.

Previous neuroscientific evidence produced with various methodological approaches (e.g., Bettencourt, & Xu, 2016; Lee et al., 2016; Lu et al., 2018; Tcheslavski et al., 2018) together with the findings of the present systematic review (Chapter 2) and the encoding meta-analysis (Chapter 3), establish the involvement of the SVC in encoding of visual information in VSTM. Here, I extend this previous evidence to now include evidence from studies that employed TMS. Moreover, replicating the well-established finding of the causal involvement of SVC in encoding of visual information in VSTM provides further evidence for the validity of TMS in indeed being a suitable method to provide causal evidence for the neural activity subserving cognitive processing involved in encoding as well as maintenance of visual information in VSTM, as I discuss next.

The majority of the experiments reviewed in Chapter 2 focused on the controversial role of the SVC in the maintenance of visual information. The TMS studies investigating this question reported evidence supporting the sensory recruitment framework (Cattaneo, et al., 2012; Rademaker et al., 2017; Saad et al., 2015; Silvanto & Cattaneo, 2010; Silvanto, & Soto, 2012; van de Ven et al., 2012; Zokaei et al., 2014). In addition, the findings of the meta-analysis of the available data coming from studies inducing TMS on the SVC during the maintenance phase of the VSTM process, further support the sensory recruitment framework by showing a significant effect of TMS. However, four experiments described in three different papers reported no significant effects of TMS, presenting evidence against the sensory recruitment framewrok (Malik et al., 2015; Saad, & Silvanto, 2013; Soto & Silvanto, 2012). As previously discussed (Chapter 2), even though three of these experiments failed to find direct TMS effects on memory performance, they reported an interaction between perception and memory processes which was evident by TMS interference. Such an interaction between perception and VSTM, indicates a shared neural substrate between the two mechanisms, which is consistent with predictions by the sensory recruitment framework and my main findings (Pasternak, & Greenlee, 2005; see also Lorenc, et al., 2021; Teng & Postle, 2021).

Overall, the systematic review (Chapter 2) and meta-analyses (Chapter 3) point to the direction of an involvement of the SVC, not merely in the encoding, but also in the maintenance of visual information (Pasternak & Greenlee, 2004). My findings are not in full agreement with recent reviews, which suggest that there is insufficient evidence to support the sensory recruitment framework (Xu, 2017, 2020, 2021). These reviews were heavily reliant on neuroimaging studies that are not suitable for detecting activity silent mechanisms thus ignoring any potential involvement of SVC during memory maintenance (Masse et al., 2020; Oberauer, 2019; Rose et al., 2016; Serences, 2016; Sreenivasen et al., 2014). Considering recent evidence indicating that information in VSTM can be stored through synaptic weight changes and other activity-silent processes (Iamshchinina et al., 2021; Lorenc et al., 2018; Rose et al., 2016; Stokes, 2015; Zhang et al, 2021), it has been postulated that contemporary research should incorporate activity-silent mechanisms for studying VSTM, which in turn can reaffirm the role of the SVC during VSTM maintenance (Lorenc & Sreenivasan, 2021; Masse et al., 2020; Teng & Postle, 2021; see also Adam et al., 2021; Beukers et al., 2021). Additionally, the activity-silent processes of the SVC have been generating a lot of still unanswered questions, such as the one raised by Oberauer (2019) about whether neurally active representations are actually functionally important for maintaining information in working memory. To address these issues, I focused on studies using TMS for disrupting content-specific neural activity, thus providing causal evidence on the cognitive process subserved by activity of the brain area being targeted by TMS (de Graaf et al., 2014; Pitcher, et al., 2021; Sadrini, et al., 2011; Tapia & Beck, 2014; van de Ven & Sack, 2013). An additional explanation of the different conclusions between my findings and previous reports is the fact that many of the experiments identified here that showed an interference of TMS with the SVC during the VSTM maintenance phase were not included in those reviews. This omission on behalf of the previous reviews showcases the importance of systematically searching the literature by following established guidelines (e.g., Moher et al., 2009, Page et al., 2021).

Notably, two important methodological shortcomings of previous studies were identified through the systematic review of Chapter 2. These shortcomings related to the binocular presentation of stimuli and the use of complex stimuli in the memory array. Therefore, in Chapter 3, I designed and conducted two TMS experiments, which settled these oversights. In Experiment 1 and Experiment 2, stimuli were presented monocularly and comprised of an elemental visual feature, specifically, orientation. In these two experiments, I showed that TMS impairs VSTM task performance when induced during both early (200 ms) and late (1000 ms) visual information maintenance. The reliability of my methods were confirmed by similar inhibitory TMS effects found during perception (outcome neutral condition; Experiment 1) and by sham TMS performance comparisons (Experiment 2). These results are in harmony with the findings of the systematic review and meta-analyses and provide additional causal evidence for the involvement of the SVC in VSTM maintenance, in line with the sensory recruitment framework.

Specifically, in Experiment 1, I showed that by ensuring monocular processing of orientation stimuli presented within 15^{o} of visual angle, SVC TMS on the ipsilateral -to the eye processing the information- brain hemisphere, resulted in impaired performance in an orientation VSTM task, compared to performance in the contralateral (control) condition (cf. Cattaneo et al., 2009; Rademaker et al., 2017; van de Ven & Sack, 2012; van Lamsweerde & Johnson, 2017). Both early (200 ms) and late (1000 ms) SVC TMS that was induced during the task's two second maintenance period impaired VSTM task performance. The same effect was replicated in Experiment 2. An analogous effect was evident for TMS induced simultaneously with stimulus presentation, during VSTM perceptual processes, parallel to the established role of the SVC during visual perception (Awh & Jonides, 2001; D'Esposito & Postle, 2015; de Graaf et al., 2014; Kammer, 2007; Masse et al., 2020; Serences, 2016), which confirmed the reliability of the early and late maintenance comparison findings.

Further to replicating the results found in Experiment 1, Experiment 2 provided additional insight for the involvement of the SVC in VSTM maintenance, by introducing sham TMS. Comparisons between real and sham stimulation revealed impaired VSTM performance, which was caused by real TMS (compared to VSTM performance in the sham TMS condition). The importance of this finding is twofold. Firstly, the use of the sham coil introduces a second control condition, further to the contralateral control condition. This addition is pivotal, since it has been previously suggested that multiple control conditions need to be considered so that TMS inferences can be limited within a specific brain network (Bergmann & Hartwigsen, 2021; Duecker & Sack, 2015; Pitcher et al., 2020). Therefore, the findings from the real versus sham stimulation comparisons from Experiment 2, reverberated the evidence in favor of sensory recruitment that was evident between the stimulation site (ipsilateral vs contralateral) comparisons.

Second, to correctly interpret the direction of the TMS effects found between the ipsilateral compared to the contralateral comparisons, the sham TMS condition is essential. Previous TMS studies presented contradictory results, with some showing inhibitory TMS effects (Jia et al., 2021; Rademaker et al., 2017; Silvanto & Cattaneo, 2010; van de Ven et al., 2012; van Lamsweerde & Johnson, 2017) and others supporting facilitatory TMS effects (Cattaneo et al., 2012; Saad et al., 2015; Zokaei, Ning et al., 2014). Moreover, the exploratory meta-analysis of these studies (Chapter 3) was unable to distinguish between the direction of effects, because of the various methods employed in each experiment and due to the failure to account for monocular stimuli presentation. This insight related to the direction of effect, by the introduction of sham TMS, helps clarify the mixed results reported in the literature and shows that the observed results were indeed due to inhibitory TMS effects.

Previous work has presented mixed results regarding the TMS timing effects with some studies indicating stronger TMS effects for earlier stimulation (up to 200 ms; Rademaker et al., 2017; van Lamsweerde et al., 2017), compared to later stimulation (400 ms, van de Ven et al. 2012; 900 ms, Rademaker et al., 2017), however other studies indicated that TMS at 200 ms was stronger (van de Ven et al., 2012). In this thesis, exploratory analyses of data from Experiment 1 provided moderate evidence against an interaction between the site and the timing of the stimulation for the effects of TMS, while Experiment 2 provided moderate to strong evidence against any timing effects. Despite their exploratory nature, these results are aligned with the results of my meta-analyses (Chapter 3). Notably, a recent review (Xu, 2017) argued that the stronger effects for earlier TMS found in some previous studies (Rademaker et al., 2017; van Lamsweerde et al., 2017) can be taken as evidence against the storage of information by the sensory visual cortex during VSTM. This argument was further complemented by the null finding in the study of van de Ven et al. (2012) for TMS at 400 ms. However, I argue that a weaker effect during later stimulation does not correspond to the absence of an effect. Contrary, as reflected by my results, even though the likelihood of the evidence is lower for later stimulation, the effects of TMS cannot be differentiated based on timing of the stimulation (see also Chapter 3). Along these lines and in contrast to the argument of Xu (2017), I propose that, taken together, evidence from TMS supports the idea that sensory visual cortex is an essential part of the network involved in VSTM.

A possible explanation of the different results concerning stimulation timings in previous TMS studies is likely attributed to the processing of information by both SVC hemispheres. Because stimuli in previous TMS work were presented binocularly, it is possible that information was processed by both the ipsilateral and contralateral SVC (Tong et al., 2006; Wichmann & Müller-Forell, 2004; Zhao et al., 2021). Since both hemispheres are employed for short-term maintenance, it is likely that feedforward and feedback mechanisms are utilized for maintenance (e.g., van Kerkoerle, 2017; for a review see Sreenivasan & D’Esposito, 2019), which can improve VSTM representation fidelity given a longer maintenance period (Goldman, 2009; Zhao et al., 2021; see also Sreenivasan & D’Esposito, 2019). In the current experiments (Chapter 4), because stimuli were restricted to enter only one SVC hemisphere, feedforward and feedback processes by binocular SVC neurons (Polonsky et al., 2010; Zhao et al., 2021) were less likely to be engaged to protect representations given the additional maintenance time. Hence, representations remained protected solely by the ipsilateral brain hemisphere, which was then susceptible to the detrimental TMS effects.

Another potential contributing factor to the lack of a TMS difference between early (200 ms) versus late maintenance (1000 ms) could be the memory load used in Experiment 1 and Experiment 2. My findings are consistent with previous research on young adults, which found that when the memory load was low, there was no difference in VSTM performance at 200 ms, 1000 ms, and even 1800 ms (Shimi & Scerif, 2017). However, when the memory load was high and exceeded VSTM capacity limits, earlier

VSTM maintenance (200 ms) was associated with better performance compared to later maintenance (1000 ms) (Shimi & Scerif, 2017). Van de Ven and colleagues (2012) also found that TMS effects on the SVC were only present when participants were required to maintain a high memory load in VSTM, but not during low memory load. This suggests that VSTM load may influence SVC activity, a conclusion supported by psychophysical (Konstantinou et al., 2014; Konstantinou & Lavie, 2013, 2020) and brain imaging evidence (Konstantinou et al., 2012, 2017).

On top of the results from the systematic review (Chapter 2) and the meta-analyses (Chapter 3), the two experiments of Chapter 4, provide additional causal evidence for the involvement of the SVC in VSTM maintenance through TMS. Between hemisphere comparisons revealed inhibitory TMS effects, as reflected by impaired VSTM task performance in the stimulated SVC hemisphere during perceptual, early maintenance, and late maintenance VSTM processes. These effects were reverberated in comparisons between sham and real TMS conditions during both early and late VSTM maintenance.

6.2.2 Insight for Sensory Recruitment Through Load Manipulation

After establishing the role of the SVC in VSTM through previous (Chapter 2) and the current (Chapter 3) TMS experiments, I implemented load manipulation in four experiments (Chapter 5) to further study the sensory recruitment framework. Previous work showed that increased VSTM load reduced the detection of irrelevant stimuli (Konstantinou & Lavie 2013) and the interference by distractors (Konstantinou et al., 2014). This reduction was specific to the sensory features of the load and differed from other types of cognitive load, such as verbal WM (Konstantinou & Lavie 2013; Konstantinou et al., 2014). These findings, together with fMRI (Konstantinou et al., 2010, 2012) and psychophysical (Konstantinou & Lavie, 2020) evidence of SVC activity interreference attributed to VSTM load, point towards a shared neural mechanism for both the memory and perception of visual stimuli, as proposed by the sensory recruitment framework (Pasternak & Greenlee, 2005; Lorenc & Sreenivasan, 2021; Teng & Postle, 2021). Along these lines, in Experiment 3, I showed the impairment of visual perception by increased VSTM load, replicating previous work (Lavie et al., 2014; Konstantinou et al., 2010, 2012, 2014; Konstantinou & Lavie, 2013, 2020) and extending their findings to show that higher VSTM load can impair the detection of an irrelevant stimulus, even if that stimulus is presented within the focus of attention.

Though, it has been argued that the limited capacity of VSTM might not be sensory specific, but instead rely upon an attentional mechanism (see Shevlin, 2020). In such a case, perceptual impairment would not be restricted within the visual modality, as predicted by the sensory recruitment framework, but would likely spread cross-modally. To rule out such cross-modal interactions, I introduced two additional experiments. In Experiments 4 and 5, I combined a delayed change-detection VSTM task with an auditory-detection task. Both experiments provided evidence for no auditory detection difference between the low and high VSTM load conditions. This finding is in agreement with the sensory recruitment framework and recent fMRI evidence that BOLD activity on the SVC or the sensory auditory cortex remained unchanged, when presenting auditory or visual input respectively (Gau et al., 2020). Additionally, my findings from Experiments 4 & 5 oppose those from perceptual research, which showed cross-modal load effects, and specifically that increased visual perception reduced the detectability of an irrelevant auditory stimulus (Macdonald & Lavie, 2011; Raveh & Lavie 2015). This contrast of findings between VSTM load and perceptual load for cross-modal, auditory stimuli indicates that, possibly, perceptual load is more susceptible to attentional capacity demands, whereas VSTM load taxes more sensory-specific demands. This could be explained by the fact that whilst perceiving information one needs to actively choose and filter, through attention, task-relevant information amongst various senses, but once this information has been perceived, the maintenance of this information has already been processed by the corresponding sensory brain area (Chai et al., 2018). Correspondingly, elemental visual features of stimuli that have been perceived and processed by the neurons of the SVC, will also rely on the same neurons for maintaining this information in VSTM, as proposed by the sensory recruitment framework (Harrison & Tong, 2009; Serences et al., 2009; Supèr et al., 2001; for reviews see Pasternak & Greenlee, 2005; Postle, 2006, 2015, 2016; Serences, 2016; Teng & Postle, 2021). Thus, it is likely that during VSTM, load effects are sensory dependent to a greater degree, compared to perceptual load, where attentional demands are increased.

Finally, in Experiment 6, I adapted the VSTM paradigm of Experiments 3, 4, and 5, to test sensory recruitment within the auditory domain. Specifically, by combining an ASTM task with an auditory-detection task, I explored whether taxing auditory load can reduce the detection of an irrelevant stimulus during the ASTM maintenance period. I found evidence of no auditory detection differences caused by ASTM load, a finding that, contrary to my predictions, does not support sensory recruitment in audition. The results of my Experiment 6 agree with a plethora of evidence showing that auditory detection remains robust across distraction and increased cognitive demand (Dalton, & Lavie, 2004; Escera et al., 2002, 2003; Kim et al., 2022; Mandal et al., 2022; Tellinghuisen & Nowak, 2003). A possible explanation lies within the view that contrary to vision, there is no physiological mechanism to completely block audition. For example, in the visual domain, eyelids can be utilised to stop visual influx, but the ears are always open to information processing. This has been partly attributed to evolution (for a similar argument see Mandal et al., 2022). Specifically, the evolutionary interpretation proposes that humans have evolved with such a mechanism, where irrelevant auditory stimuli are meant to be, almost always, processed. This can be comprehended through the example of camouflage. Many predators have developed camouflage, which makes them invisible to the naked eye. Hence, danger cannot always be seen, but noises (e.g., stepping on a branch or moving through bushes) can more consistently notify about danger and signify a response. In evolutionary terms, relying on audition is more reliable than vision for danger perception, which serves as one possible account for the robustness of auditory detection.

Throughout, my load manipulation experiments presented in Chapter 5 seem to be in harmony with the predictions of the sensory recruitment framework, at least for VSTM. My attempt to investigate sensory recruitment for ASTM provided no evidence for a shared memory and perceptual system within audition, however, there are alternative explanations for this. These alternative explanations are presented, along with other limitations of the current thesis, in the following section.

6.2.3 Limitations and Alternative Explanations

This thesis has attempted to explore the debated sensory recruitment framework by focusing mainly on TMS. TMS was chosen because, currently, it is one of the most reliable tools allowing for causal inferences (Bergmann, & Hartwigsen, 2021; de Graaf, & Sack, 2011; Hallett, 2000; Pascual-Leone et al., 2000; Pitcher et al., 2020; Sack, 2006; Sandrini et al., 2011; Siebner et al., 2009). Nevertheless, as every other available neuroscientific tool, it is still susceptible to its limitations. In detail, some factors need to be considered when interpreting TMS studies, which concern the complexity of the TMS effects, both physiologically, and then on the observable behavioral output (Bergmann, & Hartwigsen, 2021; de Graaf, & Sack, 2011; Harris et al., 2008; Pitcher et al., 2020; Silvanto & Cattaneo, 2017). As such, any effects need to be interpreted with caution. For example, both the “virtual lesion” and “neural noise” descriptions have been criticized as too simplistic and thus inadequate to describe the true complexity of the TMS effects (Bergmann, & Hartwigsen, 2021; Harris et al., 2008; Silvanto & Cattaneo, 2017), as TMS has been shown to interfere with both feedforward and feedback processes (Kim & Freeman, 2014), with activity silent mechanisms (Rose et al., 2016), with oscillatory activity (Riddle et al., 2020), between sub-cortical and intra-cortical inputs (Kim et al., 2015), and between brain regions (Ruff et al., 2008).

Physiologically, TMS on the SVC was shown to result in highly variable effects described as facilitatory or suppressive (or both) for neural activity, depending on various factors. Some of these factors include stimulation intensity (Kammer et al., 2005), stimulation duration and frequency (Aydin -Abidin et al., 2006; Eldaeif et al., 2011; Moliadze et al., 2003), eye-movements (Silva et al., 2021), and tuning properties (i.e., stimulus orientation, contrast, spatial frequency; Kim et al., 2015). Further, evidence from single-unit recordings indicated that TMS effects are state-dependent, such that greater TMS effects are expected when neural activity is higher before stimulation (Pasley et al., 2009). Similarly, these state-dependent effects have been reflected in behavioral outcomes, for example when specific visual stimuli are primed (e.g., congruent vs. incongruent primer; Silvanto et al., 2018) or when spatial attention is required (e.g., attended vs. unattended locations; Bestmann et al., 2007).

The complexity of the stimulation effects using TMS should therefore be taken into consideration when interpreting TMS studies reporting TMS effects (or lack of effects), especially when inferring the neural mechanism of such effects. For example, cognition is often viewed through a strictly modular approach, where the neural activity in a specific ROI is considered responsible for the observed behavior (e.g., the

‘Sheringtonian’ view; Barack & Krakauer, 2021). This may lead to strictly modular TMS cause-and-effect relationships between a particular ROI and an observed behavior, and consequently the neural activity in the ROI is viewed as either the cause or not, of the observed behavior. As described above, the complexity of TMS effects restricts such modular cause-and-effect inferences. Nonetheless, it is reasonable to assume that the TMS effects on the observed behavior provide causal information regarding the brain network that underlies the cognitive process under investigation (Bergmann & Hartwigsen, 2021; Pitcher et al., 2020).

This complexity of TMS effects was also reflected in the heterogeneity between the identified studies from my meta-analyses (Chapter 3). This heterogeneity was expected, given the different methodological approaches, especially regarding the different parameters of TMS stimulation (de Graaf, & Sack, 2011; Pitcher et al., 2021; Sadrini et al., 2011; van de Ven & Sack, 2013). For example, even though a difference in the direction of effects was found, indicating inhibitory TMS effects during VSTM encoding compared to the facilitatory TMS effects during VSTM maintenance, this heterogeneity between the studies limits the conclusions that can be drawn by such findings. Specifically, because TMS effects on physiology and behavior can be complex, it currently remains impossible to infer on the specific parameters driving the differences in the direction of stimulation effects. Ideally, a meta-analysis that groups each effect size according to its specific stimulation protocol and behavioral paradigm would provide important information regarding how SVC TMS interferes with VSTM performance, but unfortunately, the small number of identified studies restrict us from such analyses. It should be noted, however, that because of the small number of the identified studies, the heterogeneity tests are rather indicative, and no strong conclusions can be drawn from these.

Moreover, in Chapter 3, significant small study bias was identified, which was reflected in the asymmetry of the funnel plot and the significant statistical test for small study bias in the encoding meta-analysis. This could indicate a possible publication bias, often referred to as the file drawer problem (e.g., Nagarajan et al., 2017; see also Friese, & Frankenbach, 2019), which has been shown to be common in cognitive neuroscience (Huber et al., 2019). However, because of the small number of identified studies and the fact that almost half of these studies explored a different primary question to the one explored through my meta-analyses, no robust conclusions regarding this kind of bias can be drawn. However, it must be noted that publication bias can indeed affect the results of the meta-analysis both for the Q test, as well as the heterogeneity tests by increasing or decreasing the value of the true effect sizes (Augusteijn et al., 2019; Friese, & Frankenbach, 2019). In addition, half of the identified studies did not provide sufficient statistical data in their published work in order to be included in the meta-analyses. This limitation, of the current literature, combined with the file drawer problem, causes a drawback for meta-science and confines reproducible science. I strongly suggest that researchers and publishers, should aim to rigorously present all relevant data in their publications in order to address this concern. In general, to reduce bias scientists and journals should be encouraged to publish with a focus on robust scientific methodology as opposed to whether results are significant or not.

Regarding the evidence in support of the sensory recruitment framework, my findings oppose previous reports (e.g., Xu, 2017, 2018, 2020, 2021), which suggest that any possible involvement of the SVC during VSTM is most likely a result of feedback from higher brain areas, such as the prefrontal and posterior parietal cortex. This suggestion was based on neuroimaging data showing that VSTM representations in the SVC were wiped out at no behavioral cost, after task-irrelevant distractors were presented in a delayed estimation task (Bettencourt & Xu, 2016; but see Rademaker et al., 2019 for a different result that is in line with the findings reported here). Similar to Betterncourt and Xu's (2016) findings, brain single-unit activity measurements in non-human primates support the idea that activity in the SVC during VSTM maintenance likely reflect feedback from higher order areas (Mendoza-Halliday et al., 2014). However, considering the flexibility of the working memory system, where information can be transferred through interactions between sensory and frontal areas (Christophel et al., 2017; D'Esposito & Postle, 2015; Teng & Postle, 2021), this argument remains compatible with the idea that the sensory cortex is a necessary component of the network that underlies short-term maintenance of visual information (Gayet et al., 2018; Scimeca et al., 2018). These interactions are vital for memory maintenance in the SVC and for other attentional processes (D'Esposito, 2007; D'Esposito & Postle, 2015), meaning that activity in the frontal brain areas does not exclude or makes redundant the involvement of the SVC during memory maintenance but rather highlights that the successful short-term maintenance of visual information relies on a network of brain areas instead of activity in isolated brain areas.

An alternative explanation for the effects of TMS on memory performance reported in Chapters 2, 3 and 4, is that TMS does not interfere directly with the maintenance processes, but these effects reflect instead an interruption of attentional processes. Similar alternatives were proposed by previous reviews (Xu, 2017, 2018, 2020, 2021), suggesting that the involvement of the SVC might in fact echo feedback processing activity by higher-order brain areas (Miller et al., 1996) or deeper layers of the SVC (Van Kerkoerle et al., 2017). For example, research suggests that sensory cortices are mediated by attentional mechanisms that synchronize neural oscillations (Bauer et al., 2020). Recently, it was shown that TMS induced in different frequencies can affect VSTM performance accordingly (Riddle et al., 2020). Yet, recent research provides evidence that working memory seems to similarly rely on phase-dependent oscillations (ten Oever et al., 2020). Along similar lines, another alternative explanation of the effects of SVC TMS on VSTM performance suggests that TMS interferes with downstream processes of higher order brain areas such as the posterior parietal cortex (e.g., Xu, 2017), and not with maintenance of visual information in SVC per se. However, I think it is unlikely that my findings reflect such downstream effects of VSTM performance. Specifically, it has been systematically reported that to be able to limit inferences within a specific brain network, multiple control TMS conditions need to be considered (Bergmann & Hartwigsen, 2021; Duecker & Sack, 2015; Pitcher et al., 2021). In both Chapter 3 and Chapter 4 multiple control conditions were consider, which collectively lead to the conclusion that SVC TMS significantly affects VSTM performance, thus supporting the idea that differences on behavioral outcomes can likely be attributed to interference with SVC processing. Moreover, the comparisons between the encoding and maintenance TMS effects (the two meta-analyses and the two meta-regressions in Chapter 3, and the outcome neutral condition of Experiment 1 in Chapter 4) further support the idea that behavioral differences are not epiphenomenal but rather due to processes in the SVC. Specifically, these indicate that TMS effects during VSTM maintenance are similar to the effects during encoding, which are expected due to the established role of SVC in encoding (Awh & Jonides, 2001; D'Esposito, & Postle, 2015; de Graaf et al., 2014; Kammer, 2007; Masse et al., 2020;

Serences, 2016; Shevlin, 2020; Xu, 2017, 2020, 2021). Despite the above, because the current thesis focuses only on studies interfering with TMS on the SVC, I cannot completely rule out the possibility that such TMS behavioral effects are due to interference with downstream processes of higher brain areas such as the posterior parietal cortex. As I elaborate below (see *6.3.1 Future Sensory Recruitment Studies*) this would require the employment of double TMS paradigms, where the effects on VSTM performance can be directly compared between stimulation of the SVC and higher order brain areas (e.g., parietal cortex).

Another limiting factor concerns the direction of TMS effects. Even though the systematic review (Chapter 2) and the meta-analysis (Chapter 3) failed to draw any conclusions, the experiments in Chapter 4 established the inhibitory effects of SVC TMS during VSTM. However, facilitation TMS effects during VSTM maintenance cannot be completely ruled out. This is attributed to the possibility of different maintenance processes employed by VSTM, such as activity-silent (or latent) memory representations (Lorenc et al., 2021), and the different TMS effects on such processes (Rose et al., 2016). Specifically, previous work has discussed that the direction of TMS effects, whether inhibitory or facilitatory, depend on the attentional state of the recalled item (Silvanto & Cattaneo, 2017). For example, it has been shown that SVC TMS causes inhibitory effects for attended memory items (Zokaei, et al., 2014; Zokaei, Manohar, et al., 2014) and facilitatory effects for unattended items (Zokaei, et al., 2014; although this finding was not replicated in Zokaei, Manohar, et al., 2014). In turn, recent evidence has suggested that the attentional state can lead to different VSTM storage processes, where attended stimuli are maintained through sustained neural activations, whereas unattended items are maintained through activity-silent mechanisms (e.g., synaptic weight changes; Iamshchinina et al., 2021; for a review see Masse et al., 2020). The two experiments carried out in Chapter 4, even though they consistently revealed inhibitory TMS effects, are limited to testing the effects solely on attended -behaviorally relevant- items. However, it is possible that TMS during the maintenance of unattended items leads to opposite, facilitatory, effects (Rose et al., 2016; Zokaei, et al., 2014) but such effects remain unexplored because of the behavioral relevance of all stimuli in my task.

Finally, the behavioral load experiments presented in Chapter 5 are also subject to limitations. One such limitation concerns an alternative explanation of the opposite VSTM effects found between visual (Experiment 3) and auditory (Experiment 4 and 5) detection, related to task difficulty. Specifically, it was previously raised that impaired perception in detection tasks might not be due to VSTM load per se, but instead due to an increase of task difficulty (e.g., Konstantinou et al., 2014; Konstantinou & Lavie, 2013, 2020; see also Lavie & De Fockert, 2003). Even though such a case is unlikely to explain the VSTM load effects reported here, as reflected by the accuracy rates comparisons across experiments for both the VSTM and the detection tasks (Chapter 5), this is a limitation for ASTM load, as I will discuss below. This limitation is also related to the fact that research studying the sensory recruitment framework has remained mainly focused on vision (Adam et al., 2021; Teng & Postle, 2021; see also Shevlin, 2020). Because of this, any mechanisms underlying auditory sensory recruitment remain underexplored, due to evidence being sparse. Therefore, it is likely that, contrary to the results of Experiments 4 and 5, cross-modal interactions and auditory sensory recruitment do indeed exist but were undetected by the methods I employed in Chapter 5. This could be related to differences in the perceptual processing of visual and auditory stimuli (Jose & Kumar, 2010). Indeed, the temporal features (see Garner & Miller, 1947; Jeon & Fricke, 1997; Näätänen & Winkler, 1999; Tekman, 1997) required for the perception of visual and auditory information are different, and it is possible that the design of my ASTM and auditory-detection tasks were not appropriate to test the perception of a pure tone close to threshold levels of reaching consciousness, as was the case with visual stimuli (Experiments 1, 2 from Chapter 3, and Experiment 3 from Chapter 4). Also, evidence regarding the capacity of ASTM is very unclear and almost non-existing when it comes to pure tones, because commonly, auditory WM has been studied with stimuli consisting of semantic information, such as words (see Cowan, 1998; Fougnie & Marois, 2011; Sörqvist, 2010). Thus, even though my analyses indicated that load manipulation was successful in Experiment 6, this does not necessarily indicate that the memory array used in the high ASTM load condition was adequate to tax capacity limits. In fact, the comparison between the memory task accuracy rates across the experiments conducted in Chapter 5 indicated that the ASTM task was more difficult compared to the VSTM task, specifically in the low load condition. Thus, an alternative explanation of my findings that support a null effect, could be that ASTM was at capacity even during the low load condition. As such, the failure to find any auditory detection differences between the low and high ASTM load conditions was not because there was no effect, but because the effect remained undetected due to taxing ASTM in both load conditions. This limitation points that the findings from Experiment 6 should be taken with caution, but also showcases the need for future research to study ASTM (see *6.3 Future Directions)*.

Beyond these limitations, my thesis provides valuable insight that supports the involvement of the SVC in the neural network that supports the successful maintenance of information during VSTM. This insight provides vital foundations for forthcoming research, and it identifies important future directions. My suggestions for future work is presented next.

6.3 Future Directions

In general, I show that the SVC is involved in VSTM maintenance. This notion supports the sensory recruitment framework, which opens additional avenues for future studies, as I describe in the following sections.

6.3.1 Future Sensory Recruitment Studies

In Chapter 4, I presented a monocular orientation change-detection VSTM task, which overcomes the issues of previous TMS studies. In Experiments 1 and 2, I showed that this task is an effective method to study sensory recruitment. In detail, the task proposed in Chapter 4 can be modified and adjusted to explore the limitations that were identified here (see *6.2.3 Limitations and Alternative Explanations*) and some remaining questions that were risen from this work.

Recent views of WM seem to point towards a distributed nature of VSTM, where information maintenance relies on a whole brain network (Lorenc, & Sreenivasan, 2021; Teng & Postle, 2021). This distributed view encourages future work to focus on *how* brain areas interact in this brain network during VSTM maintenance (instead of *if* they are involved), while considering various circumstances and task demands (D’Esposito & Postle, 2015; Lorenc, & Sreenivasan, 2021; Scimeca et al., 2018; Postle, 2006, 2015, 2016; Teng & Postle, 2021). As such, to improve the understanding of the underlying brain network involved in the maintenance of information during VSTM, future work should move beyond the modular view of focusing on the contribution of a single brain area and towards the study of brain networks and functional connectivity of brain areas involved in VSTM (for similar arguments see Lorenc & Sreenivasan, 2021; Teng & Postle, 2021).

Along these lines, some alternative explanations of the sensory recruitment framework can be investigated. For instance, future research on phase-dependent cognitive mechanisms could possibly provide explanations relevant to the sensory recruitment framework. In future work, EEG could be utilized to unveil if attention and WM depend on the same oscillation phase (e.g., Arnulfo et al., 2020; Li et al., 2020) or if different frequency patterns explain each mechanism. Analogously, concerning the remaining question of SVC TMS mirroring effects from PPC downstream processes, future work could address this issue by employing double TMS paradigms. Researchers would then be able to directly compare TMS effects on SVC versus TMS on higher brain areas such as parietal cortex (e.g., Prime et al., 2008) or prefrontal cortex (e.g., Lorenc et al., 2015; see also Panichello & Buschman, 2021) during VSTM maintenance. Moreover, the monocularly presented VSTM task, can be combined with double retrospective cueing (e.g., Chen et al., 2022), which will enable the manipulation of attention between behaviorally relevant (sustained-activity) and irrelevant (activity-silent) memory items. This will allow for the investigation of possible facilitatory TMS effects and the exploration of different VSTM storage mechanisms (Lorenc et al., 2021). For instance, TMS has been shown to facilitate sustained activity in neurons that dropped to baseline activity whilst storing VSTM representations (Rose et al., 2016), and one study showed that items held in the motion sensitive area V5/MT+ are differently affected by TMS depending on their state of priority (Zokaei et al., 2014). Specifically, Zokaei et al. (2014) showed that VSTM performance for representations that were primed was inhibited due to TMS interference, while performance for unprivileged representations was facilitated due to TMS. Thus, TMS might possibly interfere differently with neurons storing representations via sustained neural activity and neurons storing representations via activity-silent mechanisms (Figure 6.1A).

As for memory load manipulations, researchers could use the monocular VSTM task and examine the effects of TMS on various VSTM memory load conditions at different stimulation timing points. Regarding the capacity limitations of VSTM, previous work indicated that under low VSTM load (memory sample consisting of one item), TMS interference during the delay had no impact on VSTM performance, but when VSTM load was high (memory sample consisting of three items) TMS impaired VSTM performance (van de Ven et al., 2012). Given that the estimated number of visual objects that can be maintained in VSTM ranges between three and four items (Cowan et al., 2005; Luck & Vogel, 1997; Todd & Marois, 2004; Vogel, et al, 2001, 2005; Vogel & Machizawa, 2004), it is therefore possible that TMS interference leaves VSTM representations unaffected when neural resources are still available (Figure 6.1B; see also de Graaf & Sack, 2011). Similarly, given that the sensory recruitment framework proposes that, beyond the storage of elemental visual features, the SVC can be flexibly employed depending on VSTM demands (Lorenc & Sreenivasan, 2021; Teng & Postle, 2021), questions about the role of the SVC during the storage of different stimuli need to be explored. For example, the experimental paradigms presented here, can be adjusted to compare the effects of TMS or VSTM load on more complex stimuli, such as faces or gazebos (e.g., Bettencourt & Xu, 2016). Also, it still remains possible that sensory recruitment generalizes to the auditory domain. Given the limited studies in the literature and the disproportional findings concerning VSTM and ASTM (Adam et al., 2021; Shevlin, 2020; Teng & Postle, 2021), it is advised that researchers invest in the exploration of the neural underpinnings of ASTM.

Figure 6. 1: Using transcranial magnetic stimulation to investigate the distributed view of the sensory recruitment framework

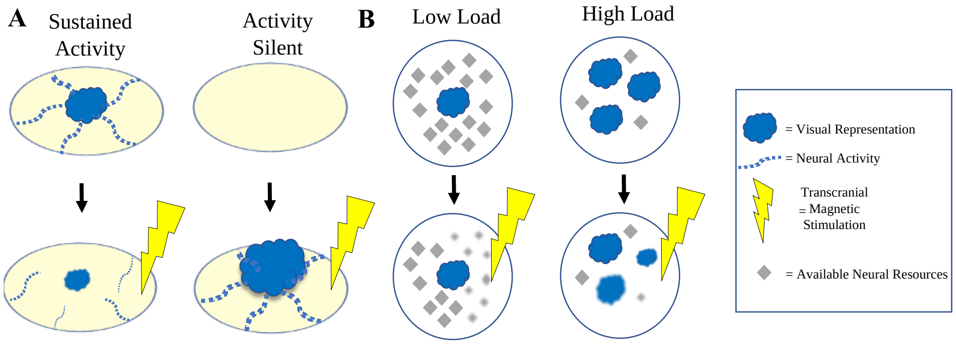


Fig.6.1. (A) Possibly, when a representation is stored through sustained neural activity mechanisms, transcranial magnetic stimulation introduces noise and disrupts storage (left). When a representation is stored through activity-silent mechanisms, transcranial magnetic stimulation facilitates representation recall by helping near-threshold neurons fire (right). **(B)** It is possible that when stored representations do not exceed sensory visual cortex neural demands (low load), enough resources are available and interference from transcranial magnetic stimulation is unable to disrupt storage (left). When stored information are close to sensory visual cortex capacity limits (high load), transcranial magnetic stimulation interferes with the stored representations (right).

Further to directing future research related to the sensory recruitment, my thesis has shed some light on general scientific issues. Thus, I next discuss how some of my findings can help guide future work, so that better scientific practices are considered.

6.3.2 Future Scientific Practices

The variety of approaches discussed (Chapter 2) and the significant heterogeneity (Chapter 3) in the TMS studies exploring VSTM, raises some important issues that ought to be discussed and addressed. In view of the live debate around the sensory recruitment framework (Ester et al., 2016; Gayet et al., 2018; Scimeca, et al., 2018; Shevlin, 2020; Teng, & Postle, 2021; Xu, 2018), I think it is fundamental to focus on reproducible practices. Specifically, future studies should focus on specific methodological and technical approaches in such a manner that between study comparisons, both qualitatively and quantitatively, can be more accurately implemented (see Hardy, & Thompson, 1998; Higgins, & Thompson, 2002; Pitcher et al., 2021). Even though such heterogeneity in methods can be viewed as supporting my conclusions (i.e., the fact that TMS produced consistent effects across a different range of protocols speaks to the generalizability of the effects), future TMS research could benefit from focusing on more reproducible and open practices. For example, future studies should aim to report all relevant results, given that even null results in TMS studies are often informative and important (de Graaf & Sack, 2011). One way of promoting this is by preregistering experiments (see Nosek et al., 2018) and by uploading the raw data sets in open repositories, such as osf.io. It is also suggested that future studies offer sufficient information regarding TMS parameters (e.g., localization, power output, coil position, frequency) in a manner which can guide and promote reproducibility (see Peterchev et al., 2012). Further, TMS studies in the field of cognitive neuroscience should carefully design their experiments (e.g., use more than one control condition) to produce more reliable results (Pitcher et al., 2021; Sadrini et al., 2011). Finally, in the next section, I draw attention to some translational directions, with a focus on clinical and computational impact.

6.3.3 Translational Impact

Recently, VSTM has been linked to deficits in various disorders such as dyslexia (Stein, 2019), schizophrenia (Yang et al., 2020), ADHD (Ortega et al., 2020), and many others (for a review see Melby-Lervåg & Hulme, 2013). Therefore, some of my findings can be used to inform clinical research. For example, VSTM deficits in psychosis have been attributed to load (Sklar et al., 2022) and to the consolidation (Fuller et al., 2009) of information. Thus, understanding the contribution of the SVC, its interaction between perception and memory, and its limitations during VSTM, is vital for the understanding of some pathology, such as psychosis. In a similar manner, my findings can be important for disorders which are related specifically to the SVC, such as blindsight (see Railo & Hurme, 2021). Along these lines, incorporating sensory recruitment in efforts of micro-stimulation to restore vision (e.g., Tehovnik et al., 2009; see also Lewis et al., 2015) is critical.

Beyond the above examples of clinical implications, my findings provide vital knowledge with an impact to technological advancements. One example is that the understanding of VSTM and sensory recruitment, can inform computational models that reflect cognition, so that they can be designed with greater efficacy and reliability (e.g., Kozachkov et al., 2022). The current lack of knowledge, for example due to the various debates in the field, such as sensory recruitment (Shevlin, 2020), restricts such reliable modelling (Reggia et al., 2019). Another technological application of my findings relates to the general understanding of TMS interference. Recent research showed that, in many cases, TMS protocols for both therapeutic (Fitzgerald, 2021) and research (Haque et al., 2021) purposes, produce unexpected results (e.g., null effects). This may be due to the lack of understanding regarding how TMS interacts with memory or perceptual representations, or due to methodological oversights, such as the failure to account for the hemisphere that processes the information or the capacity limitations of a given brain area, as was the case with the previous SVC TMS studies. Having discussed future implications of my findings for both basic and applied research, in the next and final section of this thesis, I summarize by presenting my concluding remarks.

6.4 Conclusion

In this thesis I shed light on the debated role of the SVC during VSTM maintenance. By utilizing TMS and WM load manipulations, I show that SVC draws upon a shared neural substrate for both the perception and the maintenance of elemental visual features, such as orientation and contrast, during VSTM. My findings are in harmony with the predictions of the sensory recruitment framework, which proposes that the neurons of the SVC are not only responsible for the perception of elemental visual features but are also involved during their maintenance in VSTM. The focus on TMS is critical since, with the current technological state-of-the-art, TMS is one of the most reliable methodologies that can be used to solve debates within the field of cognitive neuroscience, due to the fact that it enables scientists to draw causal inferences. Following this establishment of the sensory recruitment framework, future studies can focus on answering some of the remaining questions that have emerged, with a greater focus on *how*, rather than *if*, the SVC is involved in VSTM. Such questions concern the capacity limitations of this shared perceptual and memory neural substrate and the possible variety of neural storage mechanisms utilized by the SVC during VSTM.

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