

# **Interaction between visual perception and mental representations of imagery and memory in the early visual areas**

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## Abstract

The relationship between mental representations based on external visual percepts (i.e., information held in short-term memory or via mental imagery) and the encoding of visual input remains unsettled. What stimulates this debate is the share of overlapping neural resources between visual short-term memory (VSTM), mental imagery and visual perception in the realm of the early visual cortex (EVC). This overlap raises a number of questions: how do internal memory and imagery representations affect the perception of incoming visual information? What happens to imagery and VSTM abilities when cognitive resources need to be shared with the encoding of visual input? In short: how do visual memory/imagery and visual perception interact? This work addressed these questions by the use of behavioral paradigms coupled with transcranial magnetic stimulation (TMS) in situations where the encoding of the visual percept (measured via the tilt after effect (TAE) magnitude or the detection of sub threshold stimulus) happens either simultaneously or subsequently to holding information in VSTM/imagery.

Therefore, when VSTM and the encoding of external input occurred concurrently, VSTM maintenance was found to inhibit the visual encoding, reflected as a reduction of the TAE. Using TMS, it was shown that this inhibition takes place at the level of EVC. This reduction was found when the VSTM content matched the visual input, and when they were incongruent. However, when the encoding of external input occurred after VSTM maintenance phase had ended, VSTM maintenance was found to facilitate the former only when the VSTM content matched the visual input.

The subjective strength and the contrast of VSTM and mental imagery content (as reported by participants) affect visual detection of a briefly presented masked target. The reported visual contrast was positively associated with reporting target presence for both VSTM and mental imagery, in other words, inducing a more liberal bias. However, a differential effect was found for the subjective strength of the representations. Whereas the subjective VSTM strength was positively associated with the visual detection of the target, the opposite effect was observed for imagery. Finally, TMS applied at the EVC revealed a partial dissociation in the neural basis of VSTM and mental imagery by inducing delayed responses for the former selectively. Thus, while VSTM and mental imagery share neural resources, their neural mechanisms are partly dissociable at the level of early visual cortex.

## Tiivistelmä

Visuaaliseen havaitsemiseen perustuvien mentaalisten representaatioiden (kuten informaation säilöminen lyhytkestoisessa muistissa tai kuvittelu) ja visuaalisen informaation koodauksen yhteys on pysynyt toistaiseksi ratkaisemattomana kysymyksenä. Hermostollisten resurssien limittyminen ja jakaminen visuaalisen lyhytkestoisen muistin (VSTM; visual short-term memory), kuvittelun sekä varhaisen visuaalisen aivokuoren (EVC; early visual cortex) välillä herättää lukuisia kysymyksiä: Kuinka sisäinen muisti ja kuvittelun representaatiot vaikuttavat saapuvan visuaalisen informaation havaitsemiseen? Kuinka vaikuttaa kuvitteluun ja visuaaliseen lyhytkestoiseen muistiin, kun kognitiivisia resursseja täytyy jakaa saapuvan visuaalisen informaation koodauksen kanssa? Lyhyesti sanottuna: Kuinka visuaalinen muisti/kuvittelu ja visuaalinen havaitseminen ovat vuorovaikutuksessa keskenään? Tässä työssä vastataan yllä esitettyihin kysymyksiin yhdistämällä behavioraalisia paradigmoja transkraniaalisen magneettistimulaation (TMS) asetelmissa, joissa visuaalinen havaitseminen (TAE-vaikutuksen avulla mitattuna; tilt after effect) tapahtuu joko samanaikaisesti informaation ylläpidon VSTM:ssa/kuvittelun kanssa tai sen jälkeen.

Kun VSTM ja saapuvan ulkoisen informaation koodaus tapahtuivat samanaikaisesti, VSTM:n ylläpidon havaittiin inhihoivan visuaalista koodausta, mikä ilmeni ns. TAE-vaikutuksen heikkenemisenä. TMS avulla osoitettiin tämän inhihoivan vaikutuksen tapahtuvan varhaisella näköaivokuorella. Vaikutus löydettiin sekä visuaalisen lyhytkestoisen muistin sisällön ollessa yhtenevä että epäyhtenevä saapuvan visuaalisen informaation kanssa. Jos kuitenkin saapuvan informaation koodaus tapahtui visuaalisen lyhytaikaismuistin ylläpitovaiheen jälkeen, ylläpito fasilitoi koodausta VSTM:n sisällön ollessa yhteneväinen saapuvan ulkoisen informaation kanssa. Visuaalisen lyhytkestoisen muistin subjektiivinen voimakkuus ja kontrasti sekä mielessä kuviteltu sisältö (koehenkilöiden raportoimana) vaikuttavat lyhyesti esitetyn maskatun kohteen havaitsemiseen. Koehenkilöiden raportoima visuaalinen kontrasti assosioitui positiivisesti kohteeseen sekä VSTM:n että kuvittelun tapauksessa, toisin sanoen biasoituen liberaalimmin. Representaatioiden subjektiiviseen voimakkuuteen liittyen löydettiin kuitenkin erilainen vaikutus. Subjektiivisen visuaalisen lyhytkestoisen muistin voimakkuus assosioitui positiivisesti kohteen havaitsemiseen, kun taas kuvittelun sisällön kanssa tapahtui päinvastoin. Lopuksi TMS:n antaminen varhaiselle näköaivokuorelle paljasti osittaisen dissosiaation VSTM:n hermostollisen perustan ja kuvittelun välillä aiheuttamalla viivästetyn selektiivisen vasteen edellämäintulle. Näin ollen samall kun VSTM ja visuaalinen kuvittelu jakavat hermostollisia resursseja, niiden hermostolliset mekanismit ovat kuitenkin osittain eroavia varhaisen näköaivokuoren tasolla.

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## List of original publications

### Study I

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### Study II

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### Study III

Saad, E., & Silvanto, J. (2013). Contrast and Strength of Visual Memory and Imagery Differentially Affect Visual Perception. *PloS one*, 8(12), e84827.

### Study IV

Saad, E., Wojciechowska, M., & Silvanto, J. Partial dissociation in the neural bases of VSTM and imagery in the early visual cortex. Submitted.

## Abbreviations

M	Magnocellular
P	Parvocellular
LGN	Lateral Geniculate Nucleus
EVC	Early Visual Cortex
V1	Primary Visual Cortex
V2	Secondary Visual Cortex
PPC	Posterior Parietal Cortex
STM	Short-Term Memory
VSTM	Visual Short-Term Memory
VSSP	Visuospatial Sketchpad
TAE	Tilt After Effect
TMS	Transcranial Magnetic Stimulation
SDT	Signal Detection Theory



# 1 Introduction

Approximately 27% of the human cortex participates in encoding visual information from the outer world (Van Essen 2003). This cortical share for vision is reflected in the statement: “Thinking is visual” (Arnheim 1969). As the visual environment is constituted by much information, only the most important and relevant information are extracted, processed and retained in the brain.

The initial encoding of sensory information is the starting point for processes of other visual cognitive abilities, such as visual short-term memory and visual mental imagery. It is known that once retained or generated, memory and imagery representations share overlapping resources in the visual cortex (Kosslyn et al., 1999a; Cattaneo et al., 2009; Harrison & Tong, 2003, 2009; Serences et al., 2009).

However, even when the observer is engaged in processes such as working memory and imagery, the perceptual systems continue to receive new information. The fact that imagery, VSTM and the encoding of new input rely on overlapping neural resources raises a number of questions: how do the internal memory and imagery representations, which are initially based on external visual inputs, affect the perception of incoming visual information? What happens to imagery and VSTM abilities when cognitive resources need to be shared with the encoding of visual input? In short: how do visual memory/imagery and visual perception interact? This thesis will detail mental representations held in visual short-term memory and mental imagery, which are exclusively based on the encoding of recently presented external input.

## 1.1 Visual perception: Information pathway from the retina to Early Visual Cortex

Visual perception is the perceptual outcome of the brain response to external visual input; in other words, the outcome of brain’s response to information entering through the eye. This process is essential to higher-level cognitive processes because it lays the foundation to learn, visually memorise (Brown et al., 2007), and enables the ability to navigate through mental images (Bartolomeo, 2002).

After receiving perceptual input, in the form of light reflected from physical objects, the photoreceptors (or light receptor cells, i.e., cones and rods), situated at the level of the retina, convert the light energy captured by their receptive fields into an electrical signal, and transmit it to the lateral geniculate nucleus (LGN) via the optic chiasm. At the level of the LGN, ganglion cells innervated by cones will transmit the carried signal to the parvocellular (P) layers (layers 3-6) at the dorsal LGN (Kaplan, 2005). These parvocellular neurons discrimination sensitivity for fine details high spatial frequency are sensitive to

colour (Xu et al., 2001) and chromatic contrast (DeYoe & Van Essen, 1988; Livingstone & Hubel, 1988). This electrically-encoded visual information at the level of P neurons will transmit their contents to primary visual cortex layer 4C- $\beta$  via optical radiations (Livingstone & Hubel, 1988, Casagrande & Kaas, 1994 for review). Ganglion cells innervated by rods will transmit the signal to the Magnocellular (M) layers (layer 1 and 2) at the ventral LGN. Magnocellular neurons are sensitive to high contrast, motion and have low spatial resolution (DeYoe & Van Essen, 1988; Livingstone & Hubel, 1988). M neurons will send the signal via optical radiations to primary visual cortex (V1) layer 4C-  $\alpha$  (Livingstone & Hubel, 1988, Casagrande & Kaas, 1994 for review). A third less documented LGN cell class are the Koniocellular cells which are located in thinner layers found between the P and M layers (Kaplan, 2004).

### **1.1.1 Encoding perceptual features at the level of early visual cortex**

After reaching the primary visual cortex, features constituting the object such as colour, motion, and surface texture are encoded (Desimone & Duncan, 1995). Incoming information will be treated, in a parallel fashion, in different cells of the primary visual cortex, also known as V1 (Livingstone & Hubel, 1988; Felleman & Van Essen, 1991). V1 is organized in a retinotopic manner, i.e. nearby neurons have receptive fields encoding nearby locations in the field of vision. Cells at V1 level are organised in functional units called cortical columns, which are vertically organized and comprise several different neuronal populations (Hubel & Wiesel, 1974). V1 cortical columns include ocular dominance columns that are excited by input arriving from one eye (Adams et al., 2007). Within the ocular dominance columns different features-specific columns exist. The orientation column refers to neuronal population that is excited by only specific orientation. Blobs are sections of the visual cortex where groups of wave-length sensitive neurons are assembled in cylindrical shapes (Wong-Riley, 1979).

The early visual cortex (EVC) represents specific features via channels that are tuned to a particular range of orientation and/or spatial frequency (Campbell & Kulikowski, 1966; Graham, 1989; Wandell, 1995), and contrast (Avidan et al., 2002). Two main streams emanate from V1; the dorsal and the ventral stream. The ventral stream (also referred to as the “What” pathway), projects via the lateral occipital regions, includes the ventrolateral regions in the occipitotemporal cortex, and has been proposed to be responsible of object vision (Goodale & Milner, 1992). The dorsal stream (also referred to as the “Where” pathway), projects via dorsal extrastriate regions, includes regions in the dorsaloccipital and intraparietal sulcus, is implicated in spatial vision and action (Mishkin & Ungerleider, 1982), and triggers visual information to guide attention (Goodale & Milner, 1992).

## 1.2 Visual Short-Term Memory

Visual short term memory (VSTM) can be defined as the ability of maintaining and manipulating information beyond the presentation of the stimulus for a short period of time, and in the range of seconds (e.g. Baddeley & Hitch 1974). Prior to 1970s, most researches conducted on visual memory were not based on visual encoding selectively. Paradigms were based on stimuli which were either easily verbalized (i.e. a letter) and could be rehearsed on basis of their sound, or stimuli that were already represented in long-term memory (e.g., Sperling, 1960, 1963; Sperling, 1967; Cermak, 1971). Thus performance on these tasks did not purely assess visual short-term memory as the implemented stimuli were not exclusively visually encoded. The pioneering works of Philipps (Phillips, 1974; Phillips & Baddeley, 1971) established the base of visual short-term memory assessment. In his paradigms, Philipps used stimuli that were highly unlikely to be verbalized, and unlikely to exist as long-term representations. His paradigm was based on a 5 x 5 chessboard-like matrix composed of black-and white squares in a specific arrangement. Participants viewed two matrices separated with different delays (e.g. ranging from 300 ms to 9 seconds), and had to report if the two matrices were identical. With these experiments, assessing visual memories based on purely visual encoding became established.

The finding by Phillips on the existence of a selective visual memory gave rise to new models of memory. In 1974, Baddeley and Hitch, in a series of experiments, assessed the ability of holding a sequence of six digits in mind while simultaneously speaking out loud. Based on the findings they judged the multistore model of Atkinson and Shrifin (1968) as being too simple to explain the human memory system; rather, storing information was the outcome of independent functional processors that actively communicate. The Baddeley and Hitch model (1974) of working memory comprised three major components: A main central executive and two subordinate storage systems, referred to as slave systems, responsible for holding information in short-term: the phonological loop, and the Visuospatial Sketchpad (VSSP) (Baddeley & Liberman, 1980). In this model, the central executive is responsible for manipulating information held in slave stores, and ensuring bidirectional communication with the two subordinate storage systems. The phonological loop stores and maintains information in phonological forms, and the VSSP maintains visual and spatial information. The model has been updated several times and the latest version comprises an additional fourth component; the episodic buffer (Baddeley, 2000) which refers to a limited capacity store allowing the binding of information with the aim of creating integrated events.

Years later, Logie (1995) proposed two subdivisions of the VSSP inspired by earlier findings (Wilson et al., 1993). Specifically, Wilson and colleagues suggested that the organization of the visual system, and in particular the “what”/“where” pathways, could be

similarly applied to visual aspects of working memory. Logie proposed two subsidiary components of the VSSP: The inner scribe and the visual cache. Whereas the inner scribe is responsible of actively rehearsing the information related to spatial and movement stimuli, the visual cache is a passive store that stores static visually perceived objects. The visual cache is believed to rely on the posterior parietal cortex (PPC) (Todd & Marois, 2004, 2005). The segregation between spatial and visual components of the VSSP was already emerging before the fractionation of the VSSP (Tresch et al., 1993), and subsequently confirmed by many studies (Smith et al., 1995; Courtney et al., 1996; Della Sala et al., 1999; Hecker & Mapperson, 1997) supporting the idea that visually based mental codes are distinct for spatial and object components.

### **1.2.1 VSTM maintenance fidelity, capacity limit, and neural bases**

Studies investigating VSTM storage (Phillips, 1974; Phillips & Baddeley, 1971) gave rise to many questions; 1) How is the item held in memory; is it stored as a whole or rather in parts via selective storage of specific intrinsic features (i.e., spatial frequency, luminance, or contrast)? 2) When the features are stored, do these representations remain faithful to the real percept or are they modified?

The answer to these questions remains open as investigations on VSTM capacity are still ongoing. Many studies have assessed the online manipulation of VSTM content via the change detection task. Luck and Vogel (1997) showed that participants are able to successfully maintain and accurately recall the color and the orientation of up to 4 different objects. Additionally their results revealed that several features constituting a single object (up to 4 features) are easily encoded and recalled. These results suggest that VSTM capacity is set to the number of objects rather than features (Vogel et al., 2001). Another theory which focuses on the limited pool of resources argues that as the number of item or object complexity increases, the VSTM capacity of maintenance decreases (Vogel et al., 2001; Alvarez & Cavanagh, 2004; Wilken & Ma, 2004). In other words, the higher the stimulus complexity, the less accurate the precision of encoding and maintenance becomes (Zhang & Luck, 2008). Many researchers agree with the conclusion that VSTM capacity limit reaches 3-4 items (e.g., Cowan, 2001; Anderson et al., 2011; Delvenne et al, 2011; Gao et al., 2011).

An attempt to explain the results was introduced by Magnussen and colleagues (1996) who suggested the existence of different memory stores; each responsible of the encoding of a specific feature. Hence features are more easily stored when they form a single object (Xu et al., 2002a; 2002b). Recently, Hardman and Cowan (2014) re-discussed the storage capacity in visual memory. Based on a series of studies they found a consistent effect of features load on the visual limit storage in visual memory. Thus the authors conclude that

both the number of objects and the relevant features of those objects determine the limit of the storage.

In order to be held in VSTM the information needs to be monitored and safeguarded against interference (Postle 2005; Bor et al., 2003; D'Esposito et al., 1999). This happens via attentional selection of important information (Lebedev et al., 2004; Sakai et al., 2002) a process supported by the prefrontal cortex. At the level of the early visual cortex, the maintenance of visual features evokes sustained neural activity (cf: sensory recruitment hypothesis Awh & Jonides 2001; Postle, 2006; Ester et al., 2009; Serences et al., 2009; Harrison & Tong, 2009; D'Esposito, 2007; Riggall & Postle, 2012). The role of the prefrontal cortex in distractor and interference control has been demonstrated in patient studies; prefrontal lesions impair VSTM only when many distracters are present (D'Esposito & Postle, 1999; Thompson-Schill et al., 2002). A growing number of evidence suggests a role also for the posterior parietal cortex (PPC) in VSTM encoding and maintenance (Berryhill, 2012). For example, Todd and Marois (2004) found that activity in the PPC was correlated with the amount of information retained in VSTM. Therefore, the PPC appears to be the neural substrate of the limited VSTM retention capacity (Todd & Marois, 2004; 2005). Additionally, the capacity limit of items held in short-term memory (STM) has been shown to be mediated by competition for space in the anatomically delimited visual maps (Franconeri et al. 2013), which recently was found to be larger in individuals with a higher visual working memory capacity (Bergmann et al., 2014).

### **1.2.2 How do VSTM and external visual input interact?**

Visual short-term memory induces activity in modality-specific (Slotnick, 2004), feature-specific (Postle et al., 2004), and domain-specific (Caramazza & Shelton, 1998) regions that processes incoming visual information; the content of VSTM can be decoded from the activity patterns of the visual cortex (Harrison & Tong, 2009; Serences et al, 2009; Emrich et al, 2013) during the maintenance phase (Pasternak & Greenlee, 2005). Given this overlap in neural resources, how do VSTM and the processing of incoming visual information interact? Maintaining numerous items in VSTM has been shown to impair the detection of concurrently presented visual targets (Konstantinou et al., 2012). The opposite pattern is observed when a single item is maintained as perceptual sensitivity increases during VSTM maintenance when its contents match the visual target (Ishai & Sagi, 1997; Soto et al., 2010). Therefore VSTM maintenance can boost visual processing of matching items by enhancing the baseline activation level of early perceptual representations (Soto et al., 2010; Soto et al., 2012). Additionally, transcranial magnetic stimulation applied during the early maintenance of VSTM reveals that VSTM maintenance is able to modulate the pattern of visual activation reaching awareness (Silvanto & Cattaneo, 2010).

How does external input affect memory? In memory masking studies, a distractor is presented during the maintenance period, with the aim of assessing how the features of the distracter affect memory fidelity. Memory masking studies conducted on spatial frequency (Magnussen et al., 1991; Magnussen, 2009) and orientation maintenance (Silvanto & Soto, 2012; Bona et al., 2013) show that disruptive effect of a distractor is high when the spatial frequency/orientation of the maintained cue differs from that of the distractor. Specifically, the larger is the difference in spatial frequency/orientation between the memory item and the distractor, the stronger the disruption (Magnussen et al., 1991; Magnussen, 2009; Silvanto & Soto, 2012; Bona et al., 2013). This has been explained in terms of the distracter activating a different orientation or spatial frequency channel than the one engaged in VSTM maintenance, thus inducing inhibitory competition between the channels (e.g. Magnussen et al., 1991).

### **1.3 Mental Imagery and its neural basis**

Mental imagery is often described as “visualizing,” “seeing in the mind's eye,” “hearing in the head,” “imagining the feel of”. In other words, it refers to a conscious experience resembling sensory experience occurring in the absence of perceptual input (Kosslyn, 1994). Mental images are the “artwork” of the brain as it reconstructs the spatial geometry of the object in the absence of perceptual input (Kosslyn, 1994). It is distinct from sensory perception that involves the encoding and perception of external input. In everyday life, imagery is used when answering questions such as “what is the colour of the shirt you wore yesterday? Responding to such question often involve visualizing the object and then focusing on the attributes in question. Mental images can arise in two ways: information stored in long-term memory can be activated, or the mental image can be formed from recently presented visual information (e.g. Kosslyn et al, 2001). This thesis will detail imagery representations based on the encoding of recently presented external input.

The pioneering work in mental imagery research field took place in the early 1900's. In 1910, Perky instructed her participants to fixate at a screen and to visualize a certain object (e.g. a banana, a tomato, a leaf, an orange, or a lemon). Unknown to the participant, during their imagery, pictures of the same items were projected onto the screen. Participants never reported perceiving the items on the screen, even though items were presented above normal vision threshold, such that they were always detected when participants were not engaged in imagery. This indicated that imagery suppresses the detection of external input. The replication of the experiment (Segal & Nathan, 1964; Segal, 1971) provided further information on the interaction between imagery and the encoding of external input. Segal asked her participants to imagine New York skyline; during imagery, faint pictures of a tomato were projected onto the screen. The result revealed that participants incorporated the tomato into their imaged skyline without noticing that it was not the product of their

own imagination; specifically, observers reported New York skyline at sunset, thus incorporating the red colour into their mental image. Segal concluded that this confusion is mainly due to an overlap in neural bases between imagery generation and perception. In summary, visual imagery leads to an increase of the perceptual detection thresholds, but sometimes the visual input is incorporated into the mental image (Segal, 1971; Segal & Fusella, 1971).

Once generated, mental images are stored in a topographically organized area (due to the shared neural substrate with perception) known as the visual buffer (Kosslyn, 1980, 1994; Kosslyn & Thompson, 2003; Kosslyn et al., 2006) located in the early visual cortex. The visual buffer transfers its content into the visual cache (described above in VSTM section), which is responsible for both the encoding and the maintenance of short-term visual representations and mentally generated images (Logie 1995). The maintenance of mental images is very effortful as the resolution of the image starts to blur (starting with the edges of the object) and decays very quickly (Kosslyn, 1975, 1980), with an average duration of only 250ms (Kosslyn 1994). The fast decay of the image requires an urgent and continuous re-activation of the visual memory representations (Kosslyn, 1980; Kosslyn et al., 2006). Therefore it becomes dependent on attentional resources (Logie & Salway, 1990; Pearson et al., 1996; Salway & Logie, 1995), and thus implicates the central executive (Pearson et al., 1999) of working memory. VSTM representations and visual imagery may rely upon a common 'depictive representation' system, as visual imagery is disrupted by the maintenance of an object held within visual short-term memory (Borst et al., 2012). Therefore, the capacity limit of the visual buffer is similar to that of the VSTM (Kosslyn 1975). The third phase in mental imagery is image inspection. After being generated and maintained the mental image is interpreted in the sense that it inspects object's features and spatial properties (Kosslyn et al., 2001). Image transformation and manipulation is the fourth phase of mental imagery, and it refers to the manipulation of the image such as mental rotation (Shepard & Cooper, 1982) or the reconstruction of the image (Reisberg & Logie, 1993).

The early visual cortex has been shown to be involved in visual imagery. In a task used by Kosslyn and co-workers (1995), participants were asked to visualize line drawings of objects of different size while blindfolded; activity in the early visual cortex was associated with this task. Early visual cortex activation was observed also in a subsequent study (Kosslyn et al., 1999a) during which participants had to memorize four quadrants of black and white strips and eventually visualize these shapes (Kosslyn et al., 1996). This is important, because if mental imagery involves the early visual cortex, then it might affect the encoding of external input in this region. This may explain the suppressive effect of imagery on visual detection.

A growing amount of evidence points to mental imagery as a function of visual association cortex as it is found to be associated with neuronal firing in the same neurons that are activated by the visual presentation of those stimuli (Kreiman et al., 2000). This

interference is mainly due to the competition between imagery maintenance and visual perception for a limited pool of resources (Farah, 1989). Besides the role of EVC during image generation phase (Farah et al., 1988; Mellet et al., 1995), an increase of visual cortex excitability, by transcranial magnetic stimulation of the EVC, during imagery maintenance has also been reported (Sparing, 2002).

The effects of imagery on subsequent perceptual detection revealed two directional modulations of mental imagery interference with visual perception. The Perky effect (described above) revealed that the spatial overlap between the mental image and the visual target induces reduction in target energy (Craver-Lemley & Reeves 1992), and an increase of the perceptual detection thresholds (Segal, 1971; Segal & Fusella, 1971). Facilitation in visual perception has also been reported; however these effects have been explained in terms of priming and bias effects (Farah et al., 1998).



## **2 Aims of the study**

### **Effects of VSTM maintenance on subsequent and concurrent visual perception (Studies: I & II)**

#### **Study I**

The aim of study I was to examine how active VSTM maintenance affects subsequent visual processing. For this purpose we developed a *sequential adaptation paradigm* in which the first half of each trial involved VSTM maintenance, and the second half involved visual adaptation. (Visual adaptation was used as a measure of visual encoding efficacy). Previous studies using *concurrent* paradigms have shown an enhancement of tilt after effect (TAE) when memory cues and adapter were of similar orientation and reduction when the two differed (Greenlee & Magnussen, 1988). We thus posited that if VSTM maintenance induces effects similar to that of summation observed by two sequential visual stimuli (Greenlee & Magnussen, 1988) then its effects should summate with the subsequently presented adapter.

#### **Study II**

The aim of this study was to investigate how VSTM maintenance influences the encoding of visual input in the absence of prioritization of the latter. In previous studies assessing the impact of VSTM on visual encoding, the impact was measured in the form of how detection of a briefly presented external stimulus is affected by concurrent VSTM maintenance. Such a paradigm prioritises the encoding of external input, as high performance accuracy is encouraged. Here this was not the case; rather, we used the TAE as a measure of the magnitude of the visual encoding during VSTM maintenance. We expected that the magnitude of the TAE will depend on how VSTM maintenance affects simultaneous encoding of visual input. Therefore, if VSTM enhances encoding, the magnitude of the TAE should be increased. The opposite pattern of results should be observed if VSTM inhibits the encoding of visual input. TMS experiments were also carried out in order to investigate whether the interaction between VSTM content and the TAE occurs at the level of early visual cortex.

## **Dissociating VSTM and mental imagery at EVC, and in visual detection paradigm (Studies: III, IV)**

### **Study III**

Study III aimed to assess the strength and the visual quality of VSTM and mental imagery maintenance on subsequent visual perception. In order to understand if these effects may be independent of any subjective experience or might correlate with visual detection, We used a detection task during which observers were engaged either in VSTM maintenance or visual imagery of a similar grating. Subjective experience of memory/imagery was assessed by the use of a scale ranging from 1 to 9. Additionally, the visual quality of the memory/imagery content was assessed by asking participants to match the contrast of their memory/mental image to exemplars of gratings presented at the end of the trial.

### **Study IV**

This study aimed to assess whether a dissociation in the neural bases of mental imagery and visual short-term memory is present in the early visual cortex (EVC). For this purpose we applied TMS as a probe of visual cortical activation state. We assessed both the memory of the original cue and the accuracy of the mental image on a trial by trial basis. This was done during two different conditions: VSTM and mental imagery were assessed either in separate blocks or in intermixed blocks.

## 3 General Methods

### 3.1 Transcranial magnetic stimulation and visual cognition

Transcranial magnetic stimulation (TMS) is a tool for noninvasively modulating human brain activity. It differs from other widely used tools in cognitive neuroscience in that it contrasts to techniques such as functional magnetic resonance imaging (fMRI), electroencephalography (EEG) and magnetoencephalography (MEG) which *measure* brain activity, with TMS it is possible to *modulate* brain activity (Walsh & Pascual-Leone, 2003). It thus enables a direct assessment of brain-behavior relationship: if stimulation of a cortical region modulates behavior, then this indicates that the targeted region plays a causal role in that behavior.

#### 3.1.1 Physics of TMS

When the TMS coil is placed over the scalp, a rapidly change current, called eddy currents, with a peak magnetic fields as high as 2T, will pass from the coil, through the scalp, to the brain tissue. This induces changes in the resting membrane potentials by inducing electric field inside and outside the axon (Nagarajan et al., 1993). This will engender a cascade of biochemical reactions, starting with an initiation of a transmembrane potential (Rudiak & Marg, 1994) inducing a depolarization of the membrane which in turns provokes an action potential. In order to induce current within the axons, the electric field should not be even at cell membrane level. Therefore, it is important that the electric field traverses an unbent axon (i.e., orientation of the axon) or that the axon is bent under the electric field (i.e., stimulation coil orientation). The strong brief current, of up to 8 kA is discharged from the TMS machine through the stimulating coil, which generates a magnetic fast short rise pulse (approx. 0.1-0.2ms) and decays after 1ms. The faster the rise phase of the magnetic field is, the less time there is available for neurons to lose charge.

Figure of eight stimulation coils (Ueno et al., 1988) (used in the current studies) comprises two circular coils that carry current flowing in the opposite directions. The intersection of these coils bears the summation of both electrical and results a cone-shaped magnetic field (Walsh and Pascual-Leone, 2003). Therefore placing the center of the coil on the stimulation site enables a focal stimulation with a spatial resolution of 1cm<sup>2</sup> (Barker, 1999). The depth of the stimulation is 4 mm below figure of eight coil that will approximately cover an area of 7 by 6 cm, which decreases to 4 by 3 cm at 20 mm below the coil (Barker, 1999). Therefore TMS can mostly be use to study regions close to the cortical surface.

### **3.1.2 Spatial resolution of TMS**

The spatial resolution of TMS can be discussed in terms of primary and secondary effects. The primary effects are observed in the cortex directly underneath the center of the TMS coil. Mapping the visual and the motor cortex are good examples. Phosphene mapping (i.e., the ability of perceiving an illusory flash of light; described below) was reported to have a spatial resolution of 1 cm from the center of TMS coil when stimulating phosphene focus in the occipital area (Kammer, 1999). The ability of inducing muscle twitches with TMS has shown that stimulation of the motor cortex with a spatial difference of 0.5 to 1cm was enough to stimulate each of these different muscles selectively (Brazil-Neto et al., 1992). The secondary effects of TMS is observed at anatomically connected sites, therefore TMS effects spreads over connected areas via trans-synaptic activation as suggested by longer electromyography latencies induced by TMS (Amassian et al., 1990). This anatomical distance-effect induced by TMS has been supported by concurrent TMS and fMRI (Bohnin et al., 1999), and TMS and EEG (Ilmoniemi et al., 1997) studies. Specifically, in pioneering work combining TMS and EEG, Ilmoniemi et al (1997) showed that neural effect of a TMS pulse spreads to the contralateral hemisphere in approximately 10 milliseconds.

### **3.1.3 Temporal resolution of TMS**

The temporal resolution of TMS ranges between few milliseconds to seconds, depending on the stimulus parameters such as the duration, intensity and frequency of the pulse train. With single pulses and short pulse trains, temporal resolution in millisecond range is achieved. Amassian et al (1989, 1993) applied single pulse TMS over the calcarine fissure at different time windows ranging from 0 to 200ms after the presentation of trigrams of randomly chosen letters. TMS was found to impair the ability to detect the letters when applied at 80-120ms. Other studies extended these results by showing TMS disturbance effect at 40ms (Ashbridge et al, 1997). The temporal resolution of TMS can unveil, in milliseconds range, the flow of information between different cortical areas. Silvanto et al (2005) administered TMS over V1 and V2 (secondary visual cortex) or V5/MT, in different times windows, and showed that V1 feed forwards the visual information to V5/MT which, in turns, feeds back the info to V1 in order to be consciously perceived (Pascual-Leone and Walsh, 2001). When millisecond precision is not required, many studies use pulse trains consisting of 3-5 pulses (with a total duration of 300-500ms) which is applied during the experimental trial (Walsh & Pascual-Leone, 2003). Such pulse trains were used in present work.

### **3.1.4 How TMS affects the underlying neural population of stimulated areas**

TMS effects were first explained in terms of virtual lesions, which refer to TMS inducing effects akin to a brain lesion in the stimulated areas (Walsh & Pascual-Leone, 2003). However this earlier concept has been expanded as TMS effects were more considered as an online interaction between the TMS pulse and the stimulated areas (Silvanto & Muggelton, 2008; Miniussi et al., 2010). TMS is believed to act by activating neurons randomly in the targeted region, thereby adding noise to the highly organized pattern of neural activity associated with perceptual processes (see e.g. Pascual-Leone & Walsh, 2003; Ruzzoli et al., 2010). When TMS is applied during a visual perception task, an activity imbalance exists at neuronal level of the stimulated areas. Neurons that are not involved in the process are less active than those directly involved in the processing. TMS affects neural population that is less excitable or active which reduces the signal to noise ratio. Thus, a behavioural disruption is observed (Silvanto & Muggleton, 2008). Whether TMS enhances or disrupt performance could be explained by the concept of stochastic resonance (Miniussi et al., 2010) which refers to a system where the signal is too weak to be detected but can be boosted by adding noise to it, thereby lowering the response threshold of the system. Also the directional effect of TMS (i.e., facilitation or inhibition) depends on two factors; the initial state of the targeted region and the interaction between the stimulus strength and the TMS intensity. Therefore, whereas high-intensity induces impairment in discrimination of high coherent motion due to a drowning effect of added noise; low intensity stimulation facilitates the discrimination of low coherent motion by the introduction of low level noise to the system (Schwarzkopf et al., 2011).

Application of TMS over visual areas induces perceptual illusions called phosphenes. Phosphene is a visual sensation of light perception in the absence of visual stimuli that arises only when the stimulated neural population reaches a high level of excitation, in other words when the excitation of the neurons is strong enough to bypass the perceptual threshold. Therefore phosphene perception not only reflects the properties of the visual cortex (Rudiak & Mang, 1994) but also reflects its excitability level (Silvanto et al., 2007; Thilo et al., 2005; Romei et al., 2012). Studies on visual deficits show that the application of TMS at midline in the occipital area corresponds to foveally presented stimuli (Kastner et al., 1998).

### **3.1.5 TMS studies of VSTM and mental imagery**

How TMS applied over the early visual cortex affects VSTM depends on a range of factors, such as how many items are being maintained, whether distracters are present, and the time point at which TMS is applied. TMS increased reaction times when applied after the probe offset (Beckers et al., 1991) and at 200 ms into the maintenance interval during

the retention of 3 to 4 items (Van de Ven et al., 2012). In the presence of a distractor, TMS has been found to facilitate memory performance, possibly by impairing distracter encoding (Silvanto & Soto, 2012). In the clock task, TMS impaired memory performance when applied at the onset of the maintenance period but facilitated it when applied towards the end of the delay period (Cattaneo et al., 2009). TMS over the early visual cortex has been shown to impair performance in visual imagery tasks, thus implicating this region in imagery processes (Kosslyn et al., 1999b; Aleman et al., 1999; Sparing et al., 2002). The use of TMS-induced phosphenes as a measure of visual cortical excitability has revealed that engagement in imagery increases visual cortical excitability (Sparing et al., 2002).

### **3.2 Measurement of visual processing by means of visual adaptation**

To investigate the efficacy of visual encoding and perception, various paradigms can be used. Adaptation paradigms are important tools because the resulting after-effects can reveal the underlying properties of perceptual systems (Gibson & Radner, 1973; Webster, 2011); for this reason, adaptation is often referred to as the psychologist's microelectrode (Frisby, 1979). One phenomenon that reveals the magnitude of visual adaptation is the tilt after-effect (TAE). The tilt after effect is a striking visual illusion in which prolonged adaptation to an oriented visual stimulus causes subsequent stimuli to appear rotated away from the adapting orientation (Gibson & Radner 1937; Magnussen & Johnsen 1986; He & MacLeod, 2001). In other words, the viewing of an oriented stimulus causes shifts in subsequently perceived orientations i.e., prolonged adaptation to a leftward tilted grating induces the rightward vertical grating to appear rotated away from the orientation of the adaptor (Gibson & Radner, 1937; Hofmann & Biclshowsky, 1909; Kohn, 2007). At neuronal level, these adaptation effect result from suppression of neural responses in early visual cortex (EVC) near the adapting orientation. The strength of the TAE was used here as a measure of how efficiently incoming visual information is processed. The logic is that if VSTM inhibits the encoding of incoming visual information, then the TAE induced by an adapter is reduced. In other words, the adapter has a smaller effect on the early visual cortex.

## 4 General procedures

### 4.1 Stimuli

In all studies, stimuli and tasks were controlled by E-Prime 2.0 (Psychology Software Tools, Inc., Pittsburgh, PA; <http://www.pstnet.com/eprime.cfm>). Stimuli were either sinusoidal luminance-modulated gratings (with a diameter of  $6^\circ$  of visual angle; generated with MATLAB, The MathWorks, Natick, MA), or blue or red squares that were either small (diameter =  $4.5^\circ$  of visual angle) or large (diameter =  $6.5^\circ$  of visual angle), presented foveally on a gray background from a viewing distance of 57 cm. The spatial frequency of the gratings was 1.44 cycles/ $^\circ$ . Stimuli had a Michelson contrast of 0.9 for memory cue in studies I and II, of 0.3 Memory/imagery cues in study III, and of 0.3, 0.2, 0.3, 0.4, or 0.5 in study IV. Targets contrast's was of 0.12 in study III, and 0.5 for TAE probe (in studies I and II). The visual probe test in study IV differed from the Memory/imagery contrast by either  $\pm 0.06$  ("difficult" difficulty level) or 0.09 ("easy" difficulty level) of Michelson contrast. Memory cues orientations were  $\pm 20^\circ$  or  $\pm 40^\circ$  in study I,  $\pm 20$  or  $50^\circ$  in study II, and  $\pm 20$ , 30 or 40 tilted from the vertical in study III. The visual adapter orientation was of  $\pm 20^\circ$  in study I, and  $\pm 20$ , 30, 40 or  $50^\circ$  from the vertical in study II. In study III the visual target orientation was either  $\pm 20$ , 30 or 40 degree from the vertical. TAE probe (In studies I and II) was a grating tilted  $-1$ , 0 or  $+1^\circ$  from the vertical, whereas memory tests were tilted  $\pm 10^\circ$  from the vertical. The mask was a uniformly black circle with the same diameter as the gratings.

#### 4.1.1 Calculation of TAE magnitude used across studies I & II

The magnitude of the TAE was calculated by averaging responses across the three TAE probes (i.e., tilt of  $-1^\circ$ ,  $0^\circ$ , and  $+1^\circ$  from the vertical). Observers were asked to press "1" for perceived leftward tilt and "2" for perceived rightward tilt. We combined trials with leftward-tilting (i.e.,  $-20^\circ$ ) and rightward-tilting (i.e.,  $+20^\circ$ ) adapters, and thus calculated an overall TAE measure by subtracting the mean response for the rightward adapter trials from the mean response for the leftward-adapter trials.

#### 4.1.2 Measure of discriminability and bias in studies III and IV

Signal detection theory is a measure of detection and discrimination performance used by many vision scientists. The basic idea behind SDT is that it is a measure of the observer's ability to distinguish a *signal* (such as a visual stimulus) from *noise* which is always present

(Green & Swets, 1966). The sensitivity or discriminability ( $d'$ ) and bias ( $C$ ) are parameters that are calculated from the observer responses. Sensitivity ( $d'$ ) refers to the observer's ability to discriminate the signal from noise; the criterion refers to observer's tendency, independently of sensitivity, to report the target being present or absent.

The SDT calculation is based on four types of responses: *Hits*, *misses*, *false alarms* and *correct rejections*. To illustrate, in Study III participants were asked to report whether they had detected the target by a Yes/No answer. *Hits* represent trials in which participants successfully reported the presence of the target; *false alarms* denote reporting the target being present in trials where the target was absent. *Correct rejections* are the successful reports of the absence of the target whereas *Misses* are “No” responses when the target was present.

#### **4.1.3 TMS stimulation and site localization in studies (II, IV)**

Biphasic TMS train pulses (consisting of five pulses applied at 10 Hz; i.e., pulse gap of 100 ms; e.g. Ashbridge et al., 1997; Campana et al., 2002, 2006; Muggleton et al., 2003) were delivered using a Nexstim stimulator (Nexstim Ltd, in study II) or Magstim rapid2 (Magstim super Rapid Plus, Magstim company, UK, In study VI) using a figure-of-eight coil. The coil was placed tangentially on the skull. To stimulate the early visual cortex, fixed coordinates were used such that the coil was positioned 2 cm above theinion and 0.5 cm laterally, on the right hemisphere (e.g. Campana et al., 2002). In study VI, phosphene localization was used in 14 out of 23 participants where TMS targeted the phosphene locus. For these participants phosphene threshold was measured using a Modified Binary Search Paradigm (MOBS; Tyrrell & Owens, 1988). Half of the participants in experiment IV (4 in Experiment II) had their MRI scans and these were used with the neuronavigation to confirm that the location of stimulation was in the vicinity of the calcarine sulcus. TMS intensity was 45% of the maximum output of the stimulator in experiment II. During Experiment IV, TMS intensity was adjusted for each participant such that an intensity of 90% of the phosphene threshold was used. For sham TMS, the coil was placed tangentially over the central midline (above POZ electrode), with foam placed between the coil surface and the scalp to increase the distance between the scalp and the coil.



## **5 Detailed studies**

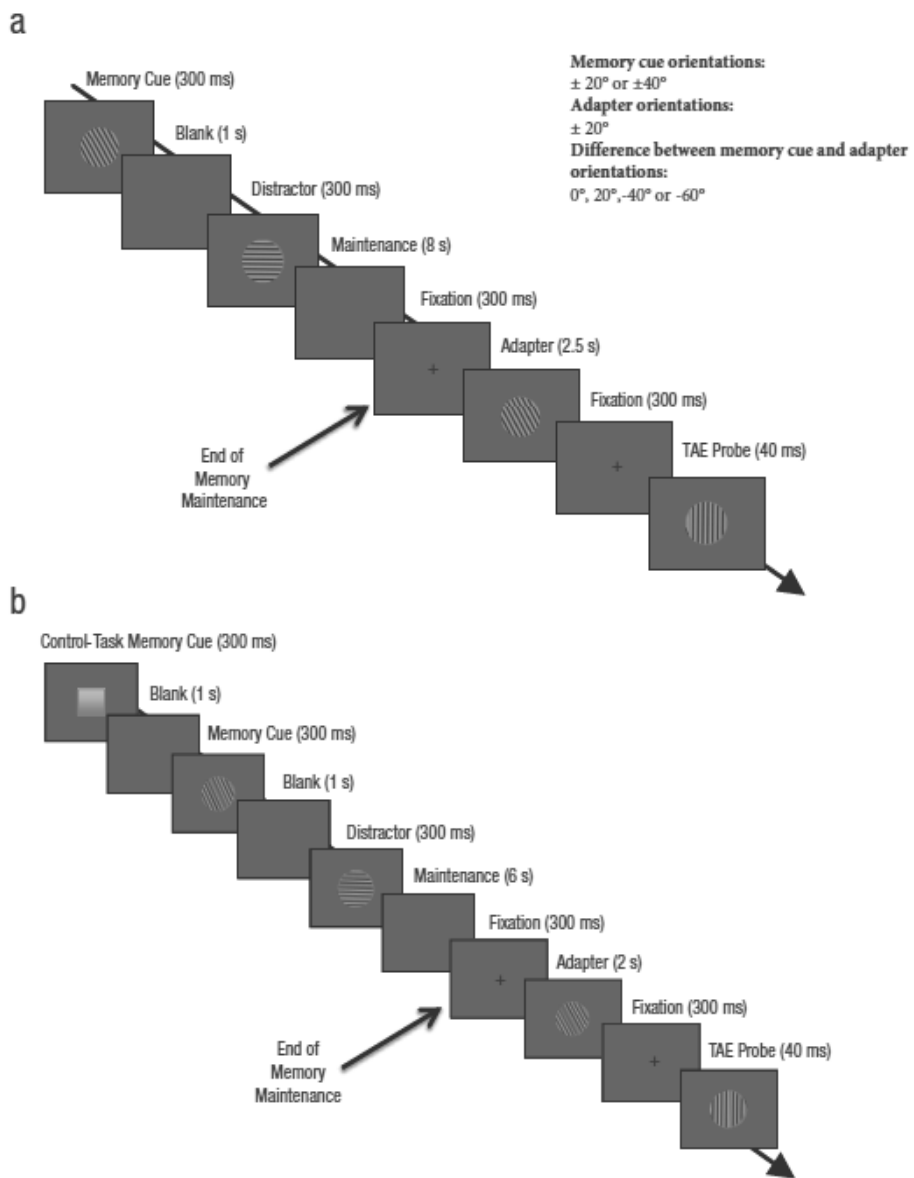
### **5.1 Study I: How Visual Short-Term Memory Maintenance Modulates Subsequent Visual Aftereffects**

Whereas the maintenance process of VSTM activates the early visual cortex (e.g., Pasternak & Greenlee, 2005), visual system sensitivity was shown to be modulated by prolonged external input as revealed by the magnitude of the TAE (Gibson & Radner, 1937; Hofmann & Bielschowsky, 1909; Kohn, 2007). This study aimed at investigating how the active maintenance of a stimulus in VSTM modulates the impact of a subsequent visual adaptation that is introduced only after that memory maintenance has ended.

#### **5.1.1 Methods**

The first half of the sequential adaptation paradigm involved an active VSTM maintenance of a grating followed by a distractor (Figure 1, Panel a). Participants were requested to hold the memory cue in mind (for  $\approx 10$ sec) and cease holding it when the fixation cross appears. The second half of the paradigm involved visual adaptation; during which an adapter was presented followed by a TAE probe. Participants were asked to report the orientation of the perceived tilt. Additional randomized memory catch trials were included to control for active maintenance.

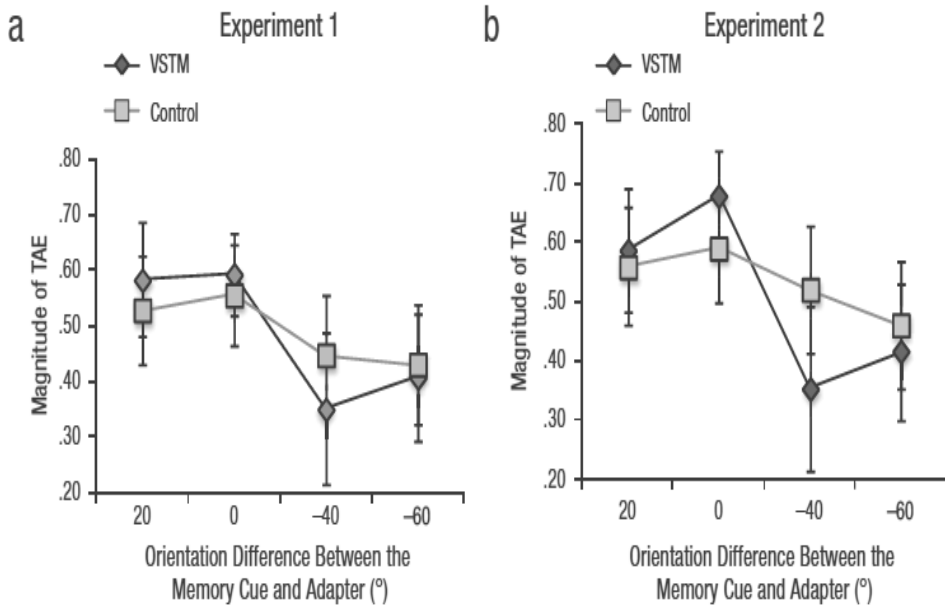
In a separate experiment (Experiment 2, Figure 1 panel 1b) we controlled for memory load by asking participants to hold in memory stimulus features that were irrelevant for the TAE. To dissociate effects induced by VSTM maintenance from effects induced by passive viewing of the stimuli, we included a control condition (in both experiments) in which participants did not have to hold in memory the memory cue. Experiments order was contour balanced.



**Figure 1** Timelines of experimental trials in the two experiments.

### 5.1.2 Results

Figure 2 (a&b) highlights the TAE magnitude induced by the visual adaptation as a function of the orientation difference between the memory cue and the visual adapter.



**Figure 2** TAE magnitude as function of the orientation difference between the memory cue and the visual adapter. Error bars indicate  $\pm 1$  SEM.

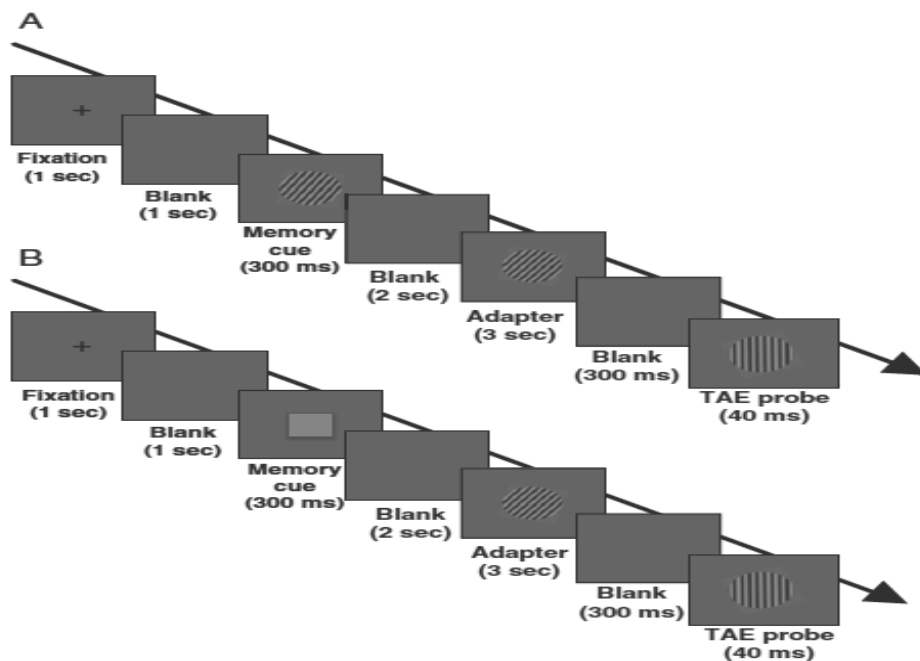
Combined analysis of Experiments 1 and 2 shows that holding actively an item in VSTM significantly increased the magnitude of the TAE induced by a subsequent visual adapter only when the memory cue orientation was congruent with that of the adapter. When the memory cue and the adapter had incongruent orientations, the magnitude of the TAE was reduced by VSTM maintenance.

## 5.2 Study II: How visual short-term memory maintenance modulates the encoding of external input: Evidence from concurrent visual adaptation and TMS

Whereas high load (numerous items) maintenance in VSTM impairs the precision of the encoding of external visual input (Konstantinou et al., 2012), lower load (single item) maintenance increases perceptual sensitivity (Ishai and Sagi, 1997; Soto et al., 2010). These paradigms however have implemented tasks that prioritized the encoding of the visual percept. Here we address the question of how VSTM maintenance modulates perception when both mechanisms are concurrently processed, and in the absence of any prioritization of the visual encoding.

### 5.2.1 Methods

Unlike Study I paradigm, in study II we used a concurrent VSTM-adaptation paradigm in which visual adaptation was carried out during VSTM maintenance (Figure 3).



**Figure 3** *Timelines of experimental trials of the experiments.*

Participants were asked to hold in mind the memory cue orientation, and at the same time, keep attending at the adapter that proceeded (after 2sec) the memory cue. The TAE was assessed afterwards by the introduction of the TAE probe. Participants were requested to report the direction of the perceived tilt. In 25% of trials we assessed memory maintenance only as no TAE probe was assessed. Baseline TAE was assessed in different blocks during which the memory cue was replaced by a black circle. In Experiment 1b three conditions were conducted: passive, shape, and baseline TAE condition. The later was identical to that of Experiment 1a. During the passive condition participants were not requested to memorize the memory cue orientation but rather to report vertical memory cues. During the shape condition, participants were asked to hold in memory a shape (which replaced the grating memory cues), and report whether the shape was 1) blue and small; 2) blue and large; 3) red and small; 4) red and large. In Experiment 1c, only 1 condition was run. In this condition the visual adapter was replaced by a black circle and the memory cue orientation ranged from  $\pm 20^\circ$  to  $\pm 50^\circ$  by steps of  $10^\circ$ . Experiment 1d, was a replication of Experiment 1a conditions with the exception of inclusion of 20% catch trials where the adapter was a vertical grating. Aims of Each of these experiments are summarized in table 1. For a detailed description on the methods please refer to study II article appended at the end of the booklet.

**Table 1** Summary of the aims of each Experiment

<b>Experiment</b>	<b>Aims</b>
<b>1a</b>	Studies the impact of concurrent VSTM maintenance of orientation information on the TAE
<b>1b</b>	Highlights the impact of: passive viewing of memory cues on the TAE concurrent VSTM maintenance of shape information on the TAE
<b>1c</b>	Investigates the impact of the VSTM maintenance on participants' responses to the TAE probe without any visual adapter
<b>1d</b>	Studies the impact of concurrent VSTM maintenance of orientation information on the TAE, while controlling the attention to the adapter
<b>2</b>	Assesses the impact of concurrent VSTM maintenance of orientation information on the TAE: TMS applied at EVC
<b>3</b>	Assesses the impact of concurrent VSTM maintenance of shape information on the TAE: TMS applied at EVC

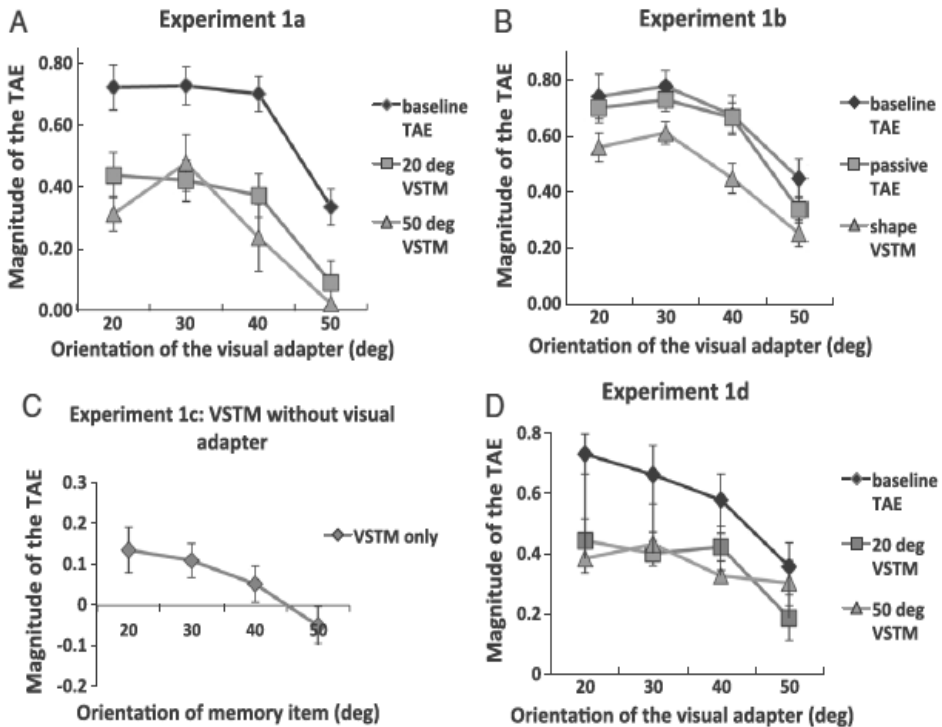
Experiments 2 included a VSTM (orientation) and a passive condition similar to those of Experiment 1a with the exception that the memory cue was only  $\pm 20^\circ$  and the adapter was

either  $\pm 20$  or  $\pm 40^\circ$ . Two TMS conditions were conducted; EVC-TMS and sham-TMS both applied at either adapter onset or adapter offset.

Experiment 3 included a VSTM (shape) and a passive condition similar to those of Experiment 1b with the exception that only two adaptation orientations were used  $\pm 20^\circ$  and  $\pm 40^\circ$ . Two TMS conditions were conducted; EVC-TMS and sham-TMS both applied at adapter onset.

### 5.2.2. Results

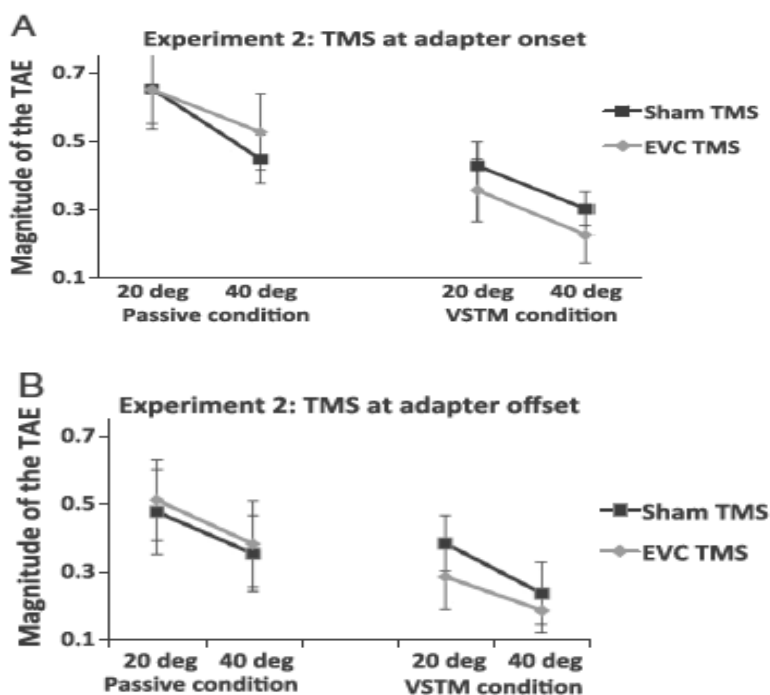
*The impact of concurrent VSTM maintenance of orientation information on the TAE (Experiments 1a), of passive viewing (Experiment 1b), in the absence of visual adapter (Experiment 1c), and when attention to the adapter is controlled (Experiments 1d).*



**Figure 4** The mean TAE magnitude ( $n=8$  in each experiment) in Experiments 1a–d. The x-axis indicates the orientation of the visual adapter (or VSTM in Experiment 1c). Error bars indicate  $\pm 1$  SEM.

The results of Experiments 1a (Figure 4A) show that: VSTM maintenance of orientation information reduced the TAE, regardless of the orientation congruency between the memory item and the adapter. Experiment 1b (Figure 4B) reveals that VSTM maintenance of shape information reduced the TAE. Additionally, the modulation of the TAE was absent during passive viewing of the memory cues. Experiment 1c (Figure 4C) reveals that in the absence of visual adaptation, VSTM maintenance induces a very small TAE. Finally Experiment 1d (Figure 4D) reveals that the effects observed in experiment 1a cannot be due to lack of attention to the adapter.

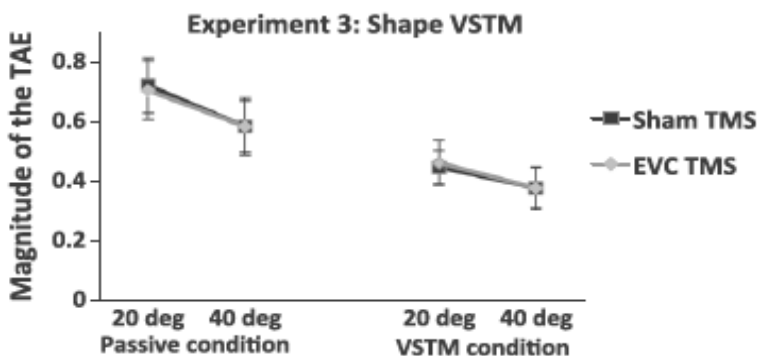
*The impact of concurrent WM maintenance of orientation information on the TAE: a TMS study*



**Figure 5** The mean TAE magnitude when TMS is applied at adapter onset (Panel A) and adapter offset (Panel B)

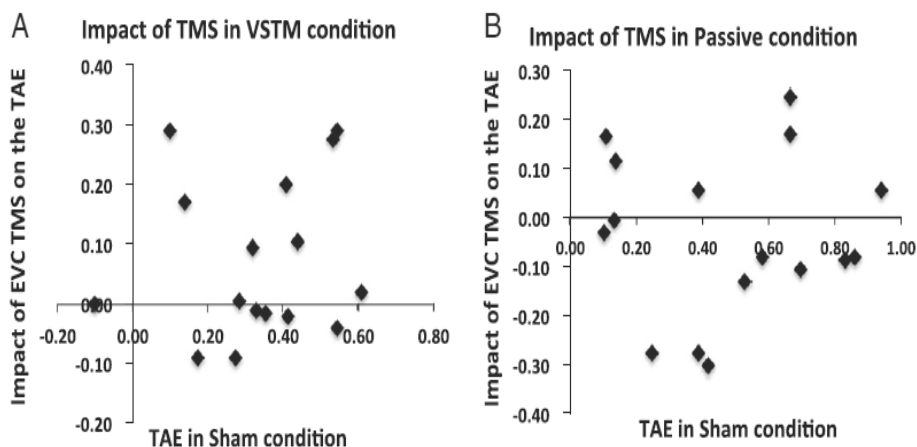
The same pattern of results was observed in both set up; i.e., when TMS was applied at adapter onset (Figure 5.A), and at adapter offset (Figure 5.B). In details, TMS applied over

the early visual cortex (EVC) reduced the magnitude of the TAE compared to Sham TMS when participants were concurrently engaged in VSTM maintenance of orientation. This pattern of results was absent during the “passive” condition, where the memory cue was not held in mind, as TMS did not modulate the magnitude of the TAE.



**Figure 6** The mean TAE magnitude when TMS is applied at adapter onset during shape maintenance

TMS applied at adapter onset during the VSTM maintenance of shape had no impact on the TAE (Figure 6). The same pattern of results was observed in both EVC TMS and Sham TMS.



**Figure 7** The magnitude of the TMS effect of each participant as a function of the “baseline” TAE (Fig. 7A: VSTM condition; Fig. 7B: passive condition).

The interaction between memory demand and TMS condition is not due to a weaker TAE in the VSTM condition rendering it more susceptible to TMS as shown by figure 7.



### 5.3 Study III: Contrast and Strength of Visual Memory and Imagery Differentially Affect Visual Perception

Whereas mental imagery interacts with visual encoding by reducing target energy (Kosslyn and Thompson, 2003), VSTM facilitates the detection of perceived information (Farah et al., 1989). However, the subjective experience underlying the impact of memory and imagery on visual encoding was never assessed on a trial by trial basis. This study aims to assess the subjective experience and the strength of the encoding for both VSTM and mental imagery during a visual detection task.

#### 5.3.1: Methods

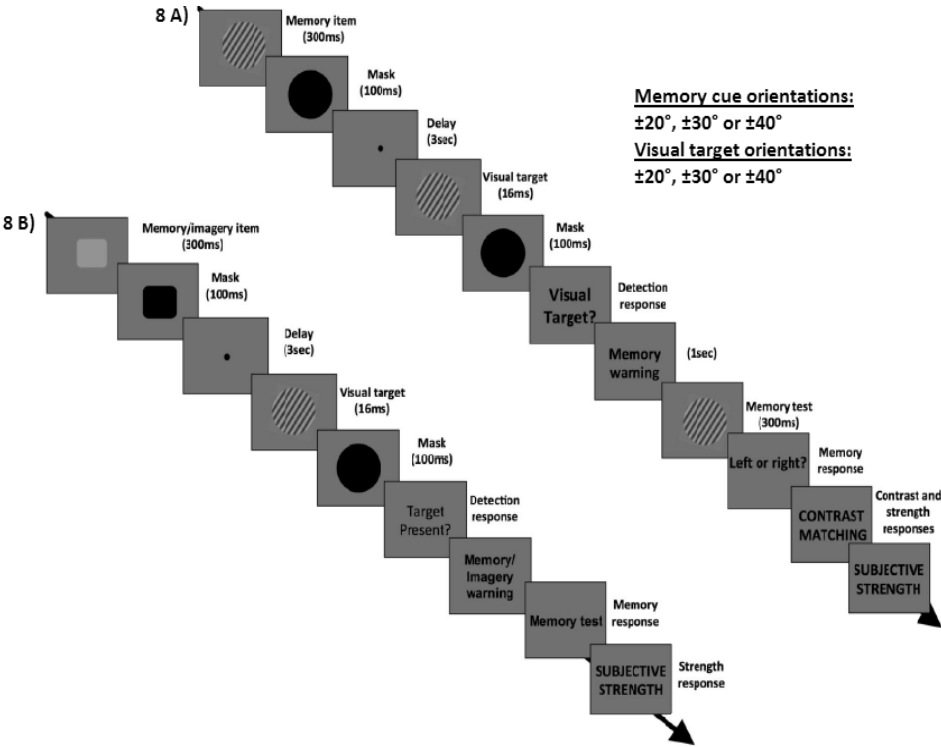
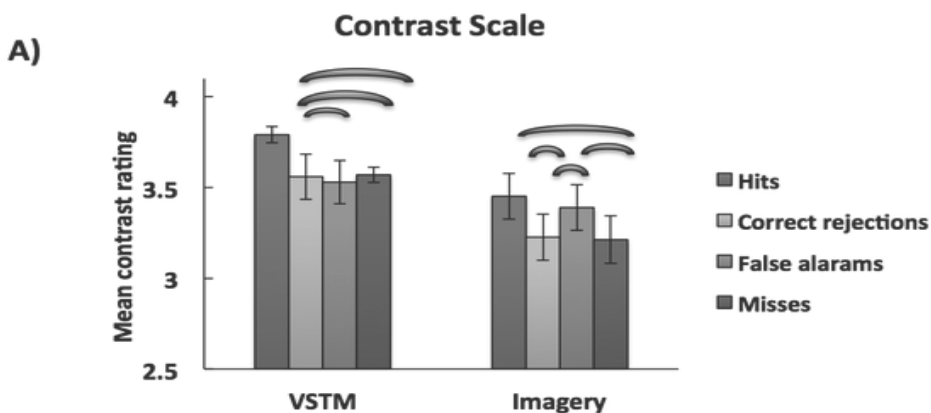


Figure 8 Timeline of an experimental trial.

Observers were asked either to hold in memory (VSTM condition) or to project their mental image of the main grating at a fixation point presented on the computer screen (imagery condition). During the maintenance, they were asked to report if they perceived a masked grating which was presented on 50% of trials. This was followed by an orientation assessment of the main cue based on the memory/imagery item. At the end of each trial, participants were asked to provide a rating of the strength of their memory or imagery on a 1-9 scale, and match the contrast of the grating held by memory/imagery to the exemplars presented on the screen (Figure 8). In Experiments 2 and 3, we assessed the impact of VSTM/imagery when the two involve items of different nature, thus VSTM/imagery involved colored shapes (rectangle) whereas the visual target was a sinusoidal grating (see figure 8B). In all the experiments we included trials in which the memory cue was replaced by a black circle in order to measure the detection of the visual target in the absence of the VSTM/imagery load.

### 5.3.2 Main Results

*Relationship between memory/imagery image contrast and detection performance*

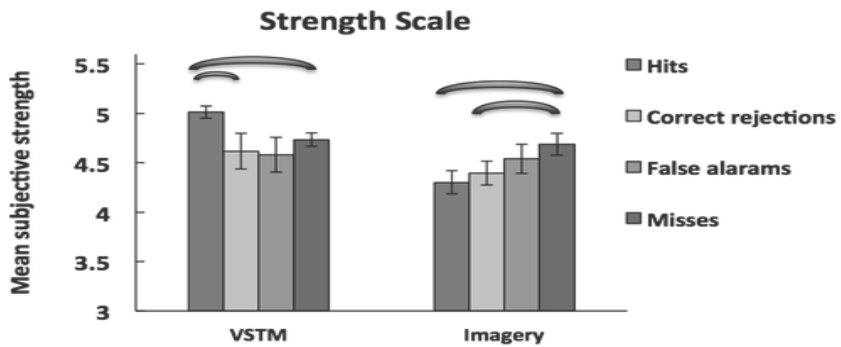


*Figure 9A Relationship between VSTM/imagery contrast (panel A) and visual detection.*

The contrast, reported by participants, for both Imagery and VSTM was positively associated with the ability to correctly report target presence (hits), such that the reported contrast was higher for hits than for misses (Figure 9A). Higher mental image contrast was equally associated to false alarms (i.e. trials on which participants tended to report target presence regardless of whether or not it was there). This indicates that participants were biased to report target presence when the mental image contrast was high.

*Relationship between subjective memory/imagery image and detection performance*

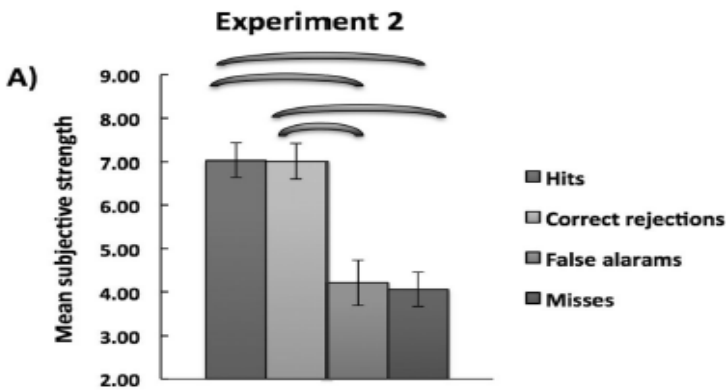
**B)**



**Figure 9B** Relationship between VSTM/imagery Subjective strength and visual detection.

Subjective strength of VSTM is positively associated with the ability to correctly report target presence (hits). In contrast, for mental imagery false responses (i.e. misses) are associated with higher subjective mental image (Figure 9B).

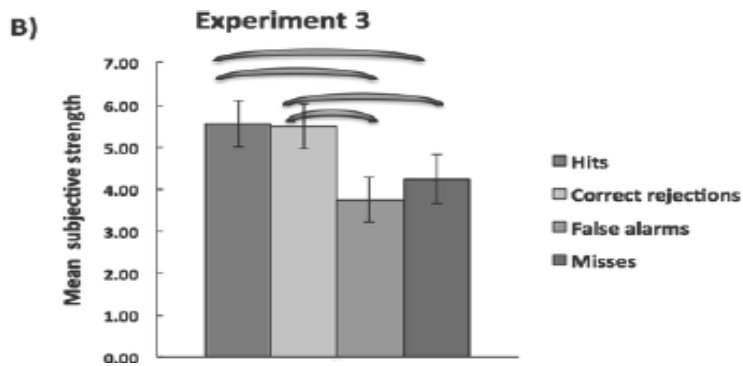
*Relationship between subjective strength of memory and detection performance*



**Figure 10 A** Mean subjective strength of VSTM in Experiment 2 as a function of performance in the detection task.

The results (Figure 10 A) show that trials on which participants tended to correctly report target presence and absence were associated with higher VSTM strength.

*Relationship between subjective strength of imagery image and detection performance*



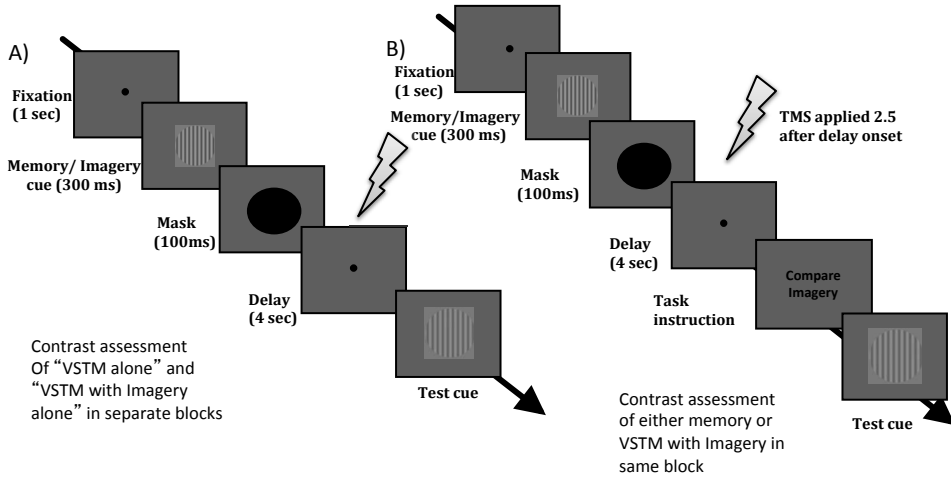
**Figure 10 B** *Mean subjective strength of mental imagery in Experiment 3 as a function of performance in the detection task.*

The results in figure 10B show that trials on which participants tended to correctly report the presence and the absence of the visual target were associated with higher mental image strength. In addition, holding in VSTM/imagery (Figures 10 A&B) a stimulus of a different class of the visual target has different effects than those observed while maintaining and perceiving identical stimulus classes.

#### **5.4 Study IV: Partial dissociation in the neural bases of VSTM and imagery in the EVC**

VSTM and mental imagery are believed to engage overlapping resources in the visual cortex (cf.; “sensory–recruitment” model of working memory; e.g. Awh and Jonides, 2001; Postle, 2006; D’Esposito, 2007). VSTM and mental imagery maintain their representations at the level of the visual cache. Thereby, the visual cache is believed to involve the EVC. This study aimed at investigating if a divergence in the neural base of the maintenance of VSTM/imagery representations happens at the EVC.

### 5.4.1 Methods

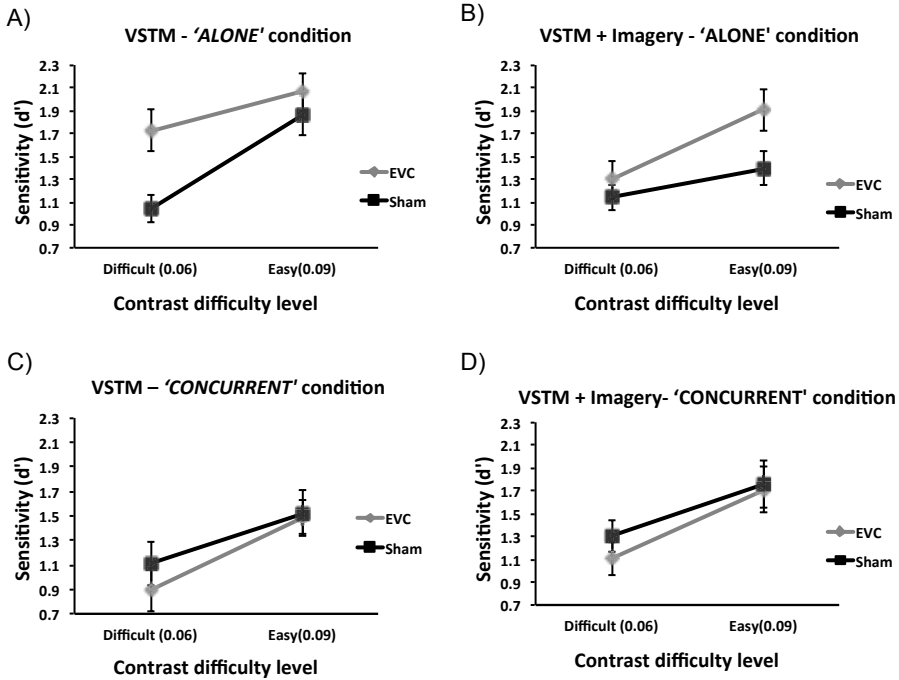


**Figure 11** *Experimental timeline in alone and concurrent blocks.*

During the alone session, Figure 11A, participants were requested to either hold in memory or form a mental image of the main cue contrast until asked to judge their own representations content by a forced choice task. Thus, to report whether the test cue contrast was lower or higher than that of their own representations (Memory or imagery) of the main cue. In the concurrent condition, figure 11B, they were requested to do both; hold in memory the main cue and form a mental image of it, until the assessment of each at the end of the trail. In both conditions TMS was applied at 2.5 sec from the 4 sec maintenance period.

## 5.4.2 Results

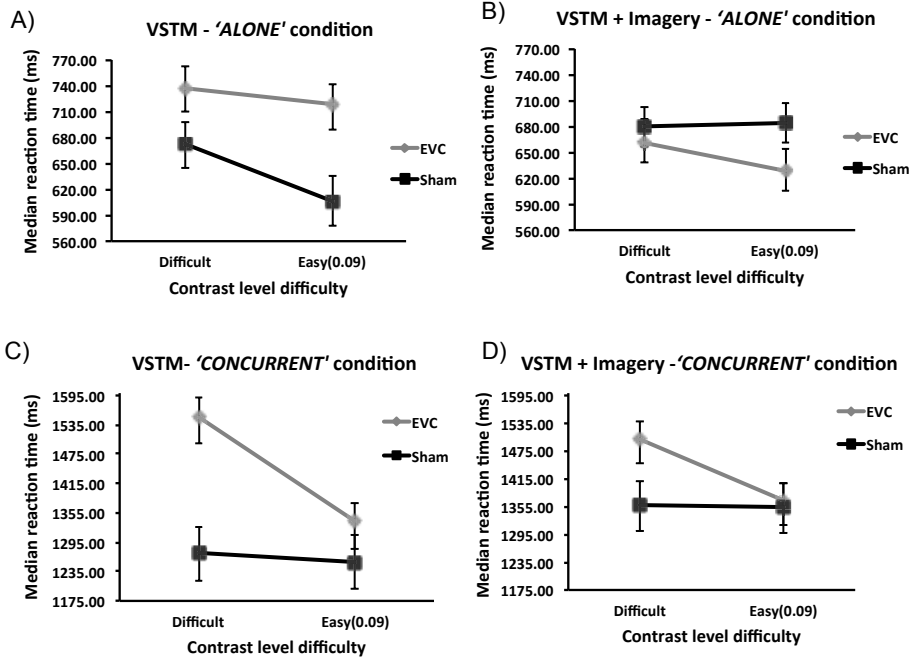
*Overall effects of VSTM and Imagery on sensitivity*



**Figure 12(a-d)** The mean ( $n=18$ ) sensitivity ( $d'$ ) for VSTM and imagery as a function of TMS site and difficulty level.

Figure 12 shows that TMS applied over the EVC facilitated the sensitivity for both VSTM and mental imagery when each was conducted alone. This effect was absent during the mixed condition as TMS had no effect on sensitivity level. Additionally, baseline performance for VSTM and imagery did not differ across conditions.

Overall effects of TMS on reaction times



**Figure 13(a-d)** The mean ( $n=15$ ) median reaction time during VSTM and imagery conditions as a function of TMS site and contrast difficulty level.

TMS applied over the EVC induced delayed responses for VSTM and therefore increased reaction times compared to the sham condition. This effect was selective to VSTM as imagery reaction time was not modulated by TMS (Figure 13).

## **6 Discussion**

### **6.1 VSTM maintenance and subsequent visual processing**

Study I has contributed to the literature by showing that VSTM maintenance can modulate the strength of subsequent visual processing, as measured here by the TAE. When the memory cue and the visual adapter orientations were congruent the TAE strength was enhanced, the opposite pattern of results was observed for incongruent orientations. These results line up with previous findings showing that visual adaptation was facilitated in paradigms where two adapters were of similar orientation and reduced when both adapters orientations differed by 30° to 60° (Greenlee & Magnussen, 1988). These effects reflect summation within and between orientation channels at the level of the early visual cortex (e.g., Blakemore & Campbell, 1969; Campbell & Maffei, 1971; Tolhurst & Thompson, 1975). The main finding of this study is that the neural effects of VSTM maintenance outlast the actual maintenance period.

### **6.2 VSTM maintenance and concurrent visual processing**

The results of Study II show that, in the absence of any prioritization of visual encoding, active VSTM maintenance reduced the efficacy of visual encoding (measured here in the form of the strength of concurrent visual adaptation). This reduction in the magnitude of the TAE is observed regardless of whether the adapter and memory cue are identical or different. The reduction of TAE was highest during orientation maintenance (*vs* shape maintenance) highlighting that the encoding of both adapter and VSTM features (orientation) was taking place at the level of same neural substrate i.e., orientation channels. Therefore these results are indicative of a competition within the orientation channels between VSTM and adapter features (e.g., Blakemore & Campbell, 1969; Campbell & Maffei, 1971; Tolhurst & Thompson, 1975). The TMS component of this study showed that the competition takes place in the early visual cortex, as real TMS has reduced the magnitude of the TAE compared to sham TMS. TMS did not modulate the TAE magnitude during passive encoding. This lines up with the mechanisms of TMS, affecting differentially non adapted and adapted neural representations (Silvanto et al., 2007; Cattaneo and Silvanto, 2008). In contrast TMS did not modulate the strength of the TAE when the maintenance was dealing with shape information. This suggests that the competition of the visual adapter and the VSTM was taking place beyond EVC, probably in the extra striate region such as the lateral occipital cortex (see e.g. Postle, 2006; van de Ven et al., 2012 for reviews). Shape maintenance inducing reduction of TAE magnitude could be explained by the involvement of fronto-parietal regions (see e.g. Feredoes et al.,



2011) revealing a competition between the VSTM content and the encoding of the adapter, therefore concurrent allocation of attention to VSTM content can reduce the TAE.

In summary, these results show that in the absence of the prioritization of the visual encoding, the encoding of concurrent visual input is inhibited during VSTM maintenance of information even when the visual input matched the VSTM content. This interaction occurs within the orientation channels at the level of the EVC pointing at a competition between VSTM and visual adapter features.

### **6.3 VSTM/imagery contrast and strength and visual detection**

The results of study III reveal that the subjective strength of VSTM and contrast of memory content positively correlated with successful visual detection performance of a stimulus presented during imagery/VSTM maintenance. In both scales the hits were associated with higher subjective strength and contrast. Therefore, the engagement in VSTM maintenance enhanced the encoding of visual input. This effect is not due to the modulation of visual detection by VSTM content fidelity as only correct memory assessment trials were included.

In opposition to these effects, subjective strength of mental imagery was negatively correlated with successful performance in visual detection (Hits). Rather, mental image strength was found to correlate with misses and false alarms. In other words, participants were more accurate in the detection task when they had a weaker mental image. These results are indicative of a competition for limited resources between mental imagery and visual perception (Farah, 1989) as the accuracy in one worsens the performance in the other. In sum, whereas VSTM subjective strength facilitates the visual perception, mental imagery worsens it.

In line with VSTM results, mental imagery contrast was associated with successful visual detection therefore individuals reporting the presence or the absence of the visual target was positively correlated to a higher contrast. However, the strength of the mental image was negatively correlated with accurate perception of the target. Thus, the weaker the mental image strength, the higher the accuracy of visual detection. However, the subjective strength of the content of VSTM/imagery and visual target when both are of different classes did not differ.

The differential effect observed for mental imagery on both scales could be explained in terms of processing level in the visual system; whereas the contrast is a low level visual feature decoded at the level of EVC, the competition between visual processing and visual imagery is more likely to take place at higher level areas.

## 6.4 Neural bases of VSTM/mental imagery maintenance

Study IV shows that TMS applied over the EVC during the maintenance of both VSTM or mental imagery enhanced the sensitivity ( $d'$ ) of these mental representations compared to sham condition. This enhancement was selective to the alone condition; i.e., when VSTM and mental imagery were conducted separately and therefore is consistent with previous findings of facilitation induced by TMS for mental imagery and VSTM (Cattaneo et al, 2009; Silvanto & Cattaneo, 2010; Silvanto & Soto, 2012). No such effect was observed during the concurrent condition. In a separate measure, TMS dissociated VSTM and mental imagery by selectively inducing delayed responses for VSTM compared to sham condition. TMS, however, had no effect on mental imagery reaction times. The qualitative divergence of the effects between sensitivity and reaction times can be explained by two different mechanisms; first TMS is believed to act by indiscriminately activating neurons in the stimulated region, therefore adding noise to the highly organized pattern of neural activity associated with perceptual processes (see e.g. Pascual-Leone & Walsh, 2003; Ruzzoli et al, 2010). Therefore as both VSTM and mental imagery sensitivity were equally modulated by TMS, the results found at the reaction times could not be due to noise affecting selectively mental imagery. Second, whereas accessing mental imagery representation is a conscious process (Logie, 1995) VSTM contents require a separate stage of retrieval to allow consciousness to access the content.

In sum, TMS enhanced the sensitivity of both VSTM and mental imagery when each was conducted alone. Additionally, TMS induced delayed responses for VSTM only. These modulatory effects were observed at the level of EVC. The differential effect on reaction times indicates that mental imagery and VSTM share overlapping resources in the EVC but their resources are yet dissociable even at low-level representations.

## 7 Conclusions

The maintenance of information in short-term memory affects the encoding of incoming visual information. The nature of this interference depends on two main factors: 1) whether both processes are engaged concurrently or not, and 2) the nature of the task.

Memory maintenance has been reported to facilitate the encoding of external input during tasks that prioritized the latter (Soto et al., 2010). However, in the prior study of Soto et al (2010), the task emphasized the importance of detecting the visual target. Similarly, in Study III of this thesis, where a detection task was used, strong subjective experience of VSTM enhanced the likelihood to report stimulus presence. However, in Study II in the absence of any prioritization of the encoding of external input (i.e. where participants were asked to view an adapter concurrently with VSTM maintenance, but where there was no task associated with this), VSTM maintenance reduced the impact of the adapter (i.e. the magnitude of the TAE was reduced). In the situation where visual processing began at the end of the memory maintenance (Study I), an enhancement of visual perception by maintenance was found (reflected as increased TAE) when VSTM contents matched the visual input. When the content of VSTM did not match the visual input, the maintenance inhibited the encoding of the external input. In summary, these studies (I and II) showed that VSTM is critical when processed before or simultaneously with visual perception as its maintenance effects can affect visual perception and these effects outlasts the end of the maintenance period.

Study IV has implications on Logie's STM model (1995). Logie proposed that both VSTM and mental imagery representations are held at the level of the visual cache in a common store. Studies III and IV challenges this view by showing dissociations in the cognitive and neural mechanisms associated with VSTM and imagery. Study III showed this at cognitive level by showing that the subjective strength of VSTM and imagery has a differential effect on visual detection. In turn, in Study IV, TMS applied over the early visual cortex differentially affected reaction times in the VSTM and imagery tasks. These dissociations are inconsistent with the view that the cognitive and neural substrate of imagery and VSTM maintenance are identical. Therefore, a theoretical contribution of this thesis is to provide evidence for a view that VSTM and imagery maintenance rely on distinct stores.

Visual hallucinations in schizophrenia (Meuser et al., 1990) hinder the ability to discriminate what is perceived from what is internally generated. Interestingly, high vividness of the mental image is a prominent trait in schizophrenia (Oretal et al., 2009, Sack et al., 2005). In healthy population, high vividness of mental imagery can be obtained by training (Sacks, 2010) and can trigger the use of mental imagery as a default cognitive strategy in memory maintenance (Keogh et al., 2014). Study III showed that higher strength of the mental image (which corresponds to vividness) alters visual perception, with

participants more likely to report stimulus present, even on target Absent trials. This has parallels with schizophrenia, in which high vividness of mental imagery may confuse the patient to infer that the internal image was externally induced.

## 8 References

- Adams, DL., Sincich, LC., Horton, JC. ( 2007). Complete pattern of ocular dominance columns in human primary visual cortex. *J. Neurosci.* 27, 10391–10403
- Aleman A., Hijman R., de Haan EH., Kahn RS. (1999). Memory impairment in schizophrenia: A meta-analysis. *Am J Psychiatry* 156:1358–1366
- Alvarez, GA., & Cavanagh, P. (2004). The capacity of visual short-term memory is set both by visual information load and by number of objects. *Psychological science*, 15(2), 106-111.
- Amassian, VE., Cracco, RQ., Maccabee, PJ., Cracco, JB., Rudell, AP., and Eberle, L. (1993). Unmasking human visual perception with the magnetic coil and its relationship to hemispheric asymmetry. *Brain Research*,605(2), 312-6.
- Amassian, VE., Cracco RQ, Maccabee PJ et al. (1989). Suppression of visual perception by magnetic coil stimulation of human occipital cortex. *Electroencephalogr Clin Neurophysiol* 74: 458–462
- Amassian, VE., Maccabee PJ, Cracco RQ, Cracco JB. (1990). Basic mechanisms of magnetic coil excitation of nervous system in humans and monkeys: application in focal stimulation of different cortical areas in humans. In: Chokroverty S, editor. *Magnetic Stimulation in Clinical Neurophysiology*. Boston: Butterworths, 1990:73 – 111
- Anderson, DE., Vogel, K., and Awh, E. (2011). Precision in visual working memory reaches a plateau when individual item-limits are exceeded. *Journal of Neuroscience*,31 (3), 1128-1138.
- Ashbridge, E., Walsh, V.,and Cowey, A. (1997). Temporal aspects of visual search studied by transcranial magnetic stimulation. *Neuropsychologia*,35(8), 1121-31.
- Atkinson, RC., & Shiffrin, R M. (1968). Chapter: Human memory: A proposed system and its control processes. In Spence, K. W., & Spence, J. T. *The psychology of learning and motivation* (Volume 2). New York: Academic Press. pp. 89–195.
- Arnheim, R. (1969). *Visual thinking*, Faber & Faber, London
- Avidan, G., Harel, M., Hendler, T., Ben-Bashat, D., Zohary, E., Malach, R. (2002). Contrast sensitivity in human visual areas and its relationship to object recognition. *Journal of Neurophysiology*, 87(6), 3102-3116.
- Awh, E., Jonides J., (2001) Overlapping mechanisms of attention and spatial working memory. *Trends in cognitive sciences* 5(3), 119-126
- Baddeley, AD., and Hitch, GJ. (1974). Working Memory. In G. H. Bower (Ed.), *The Psychology of Learning and Motivation* (Vol. 8, pp. 47–89). New York: Academic Press.
- Baddeley, AD., & Lieberman, K. (1980). Spatial working memory. In R. S. Nickerson (Ed.), *Attention and Performance VIII* (pp. 521–539). Hillsdale, NJ: Erlbaum.
- Baddeley, AD. (2000). The episodic buffer: A new component of working memory? *Trends in Cognitive Sciences*, 4, (11): 417-423.
- Barker, AT (1999). The history and basic principles of magnetic nerve stimulation. *Electroenceph. Clin. Neurophysiol. supp* 51:3-21.
- Bartolomeo, P. (2002). The relationship between visual perception and visual mental imagery: a reappraisal of the neuropsychological evidence. *Cortex*, 38(3), 357-378.

- Beckers, G., Hömberg, V., (1991) Impairment of visual perception and visual short term memory scanning by transcranial magnetic stimulation of occipital cortex. *Exp Brain Res* 87:421– 432
- Bergmann, J., Genç, E., Kohler, A., Singer, W., & Pearson, J. (2014). Neural anatomy of primary visual cortex limits visual working memory. *Cerebral Cortex*, bhu168.
- Berryhill, ME. (2012). Insights from neuropsychology: pinpointing the role of the posterior parietal cortex in episodic and working memory. *Frontiers in integrative neuroscience*, 6.
- Blakemore, C., Campbell, F.W., 1969. On the existence of neurons in the human visual system selectively sensitive to the orientation and size of retinal images. *J. Physiol.* 203, 237–260.
- Bohning DE., Shastri, A., Blumenthal, K.M., Nahas, Z., Lorberbaum, J., Roberts, D., Teneback, C., Vincent, D.J. & George, M.S. (1999). A combined TMS/fMRI study of intensity dependent TMS over motor cortex. *Biol. Psych.* 45: 385-394.
- Bona, S., Cattaneo, Z., Vecchi, T., Soto, D., & Silvanto, J. (2013). Metacognition of visual short-term memory: dissociation between objective and subjective components of VSTM. *Frontiers in psychology*, 4.
- Bor, D., Duncan, J., Wiseman, R.J., and Owen, AM. (2003). Encoding strategies dissociate prefrontal activity from working memory demand. *Neuron*, 37(2), 361-367.
- Borst, Gre, Niven E, & Logie R. (2012). "Visual mental image generation does not overlap with visual short-term memory: A dual-task interference study." *Memory & cognition* 40.3 360-372.
- Brasil-Neto, J.P., Cohen, L.G., Pascual-Leone, A., Jabir, F.K., Wall, R.T. & Hallett, M. (1992). Topographic mapping of the human motor cortex with magnetic stimulation: factors affecting accuracy and reproducibility. *Electroencephal. Clin. Neurophysiol.* 85:9-16.
- Brown, RE., and Wong, AA. (2007). The influence of visual ability on learning and memory performance in 13 strains of mice. *Learning & Memory*, 14(3), 134-144.
- Caramazza A, Shelton JR. (1998). Domain specific knowledge systems in the brain: the animate-inanimate distinction. *J Cogn Neurosci* 1998;10:1–34
- Cattaneo, Z., & Silvanto, J. (2008). Time course of the state-dependent effect of transcranial magnetic stimulation in the TMS-adaptation paradigm. *Neuroscience letters*, 443(2), 82-85.
- Cattaneo, Z., Vecchi, T., Pascual-Leone, A., & Silvanto, J. (2009). Contrasting early visual cortical activation states causally involved in visual imagery and short-term memory. *European Journal of Neuroscience*, 30(7), 1393-1400.
- Cattaneo, Z., Devlin JT, Salvini F, Vecchi T, Silvanto J. (2010) The causal role of category-specific neuronal representations in the left ventral premotor cortex (PMv) in semantic processing. *Neuroimage*. 2010 Feb 1;49(3):2728-34. doi:
- Campana, G., Cowey, A., Walsh, V. (2002) Priming of motion direction and area V5/MT: a test of perceptual memory. *Cereb Cortex* 12(6):663-9.
- Campana G, Cowey A, Walsh V (2006) Visual area V5/MT remembers "what" but not "where". *Cereb Cortex* 16(12):1766-70.
- Campbell, FW., Kulikowski, JJ. (1966). Orientational selectivity of the human visual system. *The Journal of physiology*, 187(2), 437-445.

- Campbell, F.W., Maffei, L., 1971. The tilt after-effect: a fresh look. *Vision Research* 11, 833–840.
- Casagrande, V.A., Kaas, J.H. (1994). The Afferent, Intrinsic, and Efferent Connections of Primary Visual Cortex in Primates. In: Peters, A.; Rockland, K.S., editors. *Cerebral Cortex*. New York: Plenum Publishing Co; 1994. p. 201-259.
- Cermak, G.W. (1971). Short-term recognition memory for complex free-form figures. *Psychonomic Science*, 25(4), 209-211.
- Courtney, S.M., Ungerleider, L.G., Keil, K., Haxby, J. (1996). Object and spatial visual working memory activate separate neural systems in human cortex. *Cerebral Cortex* 1996;6:39–49.
- Cowan, N. (2001). The magical number 4 in short-term memory: A reconsideration of mental storage capacity. *Behavioral and Brain Sciences*, 24, 87–114.
- Hardman, K.O., & Cowan, N. (2014). Remembering Complex Objects in Visual Working Memory: Do Capacity Limits Restrict Objects or Features?.
- Craver-Lemley C., Reeves A. (1992). How visual imagery interferes with vision. *Psychol. Rev.* 99, 633–649. [10.1037/0033-295X.99.4.633](https://doi.org/10.1037/0033-295X.99.4.633)
- Della Sala, S., Gray C., Baddeley A., Allamano N., Wilson L. (1999). Pattern span: a tool for unwelding visuospatial memory. *Neuropsychologia* 1999;37:1189–1199.
- Delvenne, J.F., Kaddour, L., and Castronovo, J. (2011b). An electrophysiological measure of visual short-term memory capacity within and across hemispheres. *Psychophysiology*, 48, 333-336
- Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual review of neuroscience*, 18(1), 193-222.
- DeYoe, E.A., Van Essen, D.C. (1988). Concurrent processing streams in monkey visual cortex. *Trends Neurosci.* 1988; 11:219–226.
- D'Esposito, M., Postle, B.R., Ballard, D., and Lease, J. (1999). Maintenance versus manipulation of information held in working memory: an event-related fMRI study. *Brain and cognition*, 41(1), 66-86.
- D'Esposito, M., and Postle, B.R. (1999). The dependence of span and delayed-response performance on prefrontal cortex. *Neuropsychologia*, 37, 1303-1315.
- D'Esposito, M. (2007). From cognitive to neural models of working memory. *Philosophical Transactions of the Royal Society B: Biological Sciences* 362(1481), 761-772.
- Ester, E.F., Serences, J.T., Awh, E. (2009). Spatially global representations in human primary visual cortex during working memory maintenance. *J Neurosci* 29:15258–15265
- Emrich, S.M., Riggall, A.C., LaRocque, J.J., & Postle, B.R. (2013). Distributed patterns of activity in sensory cortex reflect the precision of multiple items maintained in visual short-term memory. *The Journal of Neuroscience*, 33(15), 6516-6523.
- Farah, M. J., Hammond, K. M., Levine, D. N., & Calvanio, R. (1988). Visual and spatial mental imagery: Dissociable systems of representation. *Cognitive psychology*, 20(4), 439-462.
- Farah, M.J., 1989. Mechanisms of imagery-perception interaction. *J. Exp. Psychol. Hum. Percept. Perform.* 15, 203–211.
- Felleman, D.J., Van Essen, D.C. (1991). Distributed hierarchical processing in the primate cerebral cortex. *Cerebral cortex*, 1(1), 1-47.

- Farah M J, Wilson KD, Drain M, Tanaka JN (1998) What is "special" about face perception?. *Psychological review*, 105(3), 482
- Feredoes, E., Heinen, K., Weiskopf, N., Ruff, C., Driver, J., 2011. Causal evidence for frontal involvement in memory target maintenance by posterior brain areas during distracter interference of visual working memory. *Proc. Natl. Acad. Sci. U. S. A.* 108 (42), 17510–17515.
- Franconeri, L., Alvarez, GA., and Cavanagh, P. (2013). Flexible cognitive resources: competitive content maps for attention and memory. *Trends in cognitive sciences*, 17(3), 134-141.
- Frisby, J. (1979). *Seeing: Illusion, brain and mind*. Oxford, England: Oxford University Press.
- Gao, Z., Xu, X., Chen, Z., Yin, J., Shen, M., & Shui, R. (2011). Contralateral delay activity tracks object identity information in visual short term memory. *Brain Research*, 1406 ,30-42
- Graham, NS. (1989). *Visual Pattern Analyzers*. Oxford: Clarendon Press.
- Goodale, MA., Milner, AD. (1992). "Separate visual pathways for perception and action". *Trends Neurosci.* 15 (1): 20–5.
- Gibson, J. J., & Radner, M. (1937). Adaptation, after-effect and contrast in the perception of tilted lines. I. Quantitative studies. *Journal of Experimental Psychology*, 20, 453–467
- Greenlee, M. W., & Magnussen, S. (1988). Interactions among spatial frequency and orientation channels adapted concurrently. *Vision Research*, 28, 1303–1310.
- Green D.M., Swets, J.A. (1966). *Signal detection theory and psychophysics*. New York Wiley
- Harrison, SA., Tong, F. (2009). Decoding reveals the contents of visual working memory in early visual areas. *Nature* 458:632–635
- He, S., & MacLeod, D. I. (2001). Orientation-selective adaptation and tilt after-effect from invisible patterns. *Nature*, 411,473–476.
- Hecker, R., Mapperson, B. (1997). Dissociation of visual and spatial processing in working memory. *Neuropsychologia* 1997;35:599–603.
- Hofmann, F.B., Bicschowsky, A., 1909. Ober die Einstellung der scheinbaren Horizontalen und Vertikalen bei Betrachtung. *Pflfigers Arch* 126, 453–475.
- Hubel, DH., Wiesel, TN. (1974). Sequence regularity and geometry of orientation columns in the monkey striate cortex. *Journal of Comparative Neurology*, 158(3), 267-293.
- Ilmoniemi RJ, Virtanen J, Ruohonen J, Karhu J, Aronen HJ, Naatanen R, Katila T (1997). Neuronal responses to magnetic stimulation reveal cortical reactivity and connectivity. *Neuroreport* 8: 3537-3540.
- Ishai, A., Sagi, D., 1997. Visual imagery facilitates visual perception: psychophysical evidence. *J. Cogn. Neurosci.* 9, 476–489.
- Kammer T (1999). Phosphenes and transient scotomas induced by magnetic stimulation of the occipital lobe: their topographic relationship. *Neuropsychologia* 37: 191-8.
- Kastner S, Demmer I, Ziemann U. (1998). Transient visual field defects induced by transcranial magnetic stimulation over human occipital pole. *Exp Brain Res* 118:19-26.
- Kaplan, E. (2005). The m, p and k pathways of the primate visual system. In *investigative ophthalmology & visual science* (vol. 46).



- Keogh, R. & Pearson, J. (2014). The sensory strength of voluntary visual imagery predicts visual working memory capacity. *Journal of Vision*, 14 (12):7, 1-13.
- Kohn, A. (2007). Visual adaptation: physiology, mechanisms, and functional benefits. *Journal of neurophysiology*, 97(5), 3155-3164.
- Kosslyn S.M.(1975). Information representation in visual images. *Cognitive Psychology*. 1975;7(3):341–370.
- Kosslyn, Stephen M. 1980 *Image and Mind*. Cambridge, MA: Harvard University Press.
- Kosslyn, S.M. (1994). *Image and Brain: The Resolution of the Imagery Debate*. Cambridge, MA: MIT Press.
- Kosslyn, S.M., Thompson, W.L., Kim, I.J., & Alpert, N.M. (1995). Topographical representations of mental images in primary visual cortex. *Nature*, 378, 496–498
- Kosslyn, S.M., Thompson, W.L., Kim, I.J., Rauch, S.L., & Alpert, N.M. (1996). Individual differences in cerebral blood flow in area 17 predict the time to evaluate visualized letters. *Journal of Cognitive Neuroscience*, 8, 78–82.
- Kosslyn, S.M., Pascual-Leone, A., Felician, O., Camposano, S., Keenan, J.P., Ganis, G., & Alpert, N.M. (1999b). The role of area 17 in visual imagery: convergent evidence from PET and rTMS. *Science*, 284(5411), 167-170.
- Kosslyn, S.M., Sukel, K.E., Bly, B.M., (1999a). Squinting with the mind's eye: effects of stimulus resolution on imaginal and perceptual comparisons. *Mem. Cogn.* 27 (2), 276–287.
- Kosslyn S.M., Ganis G., & Thompson W. (2001). Neural foundations of imagery. *Nature Reviews Neuroscience*, 2, 635-642.
- Kosslyn, S.M., Thompson, W.L. (2003). When is early visual cortex activated during visual mental imagery?. *Psychological bulletin*, 129(5), 723.
- Kosslyn, S.M., Thompson, W.L., & Ganis, G. (2006). *The Case for Mental Imagery*. Oxford: Oxford University Press.
- Konstantinou, N., Bahrami, B., Rees, G., Lavie, N., 2012. Visual short-term memory load reduces retinotopic cortex response to contrast. *J. Cogn. Neurosci.* 24 (11), 2199–2210.
- Kreiman, G., Koch, C., & Fried, I. (2000). Imagery neurons in the human brain. *Nature*, 408(6810), 357–361.
- Lebedev, M. A., Messinger, A., Kralik, J. D., and Wise, S. P. (2004). Representation of attended versus remembered locations in prefrontal cortex. *PLoS biology*, 2(11), e365.
- Logie, R.H. (1995). *Visuo-Spatial Working Memory*. Hove, U.K.: Erlbaum.
- Logie R.H., Salway A.F.S. Working memory and modes of thinking: A secondary task approach. In: Gilhooly K.J., Keane M., Logie R.H., Erdos G., editors. Vol. 2. Wiley; Chichester: 1990. pp. 99–113.
- Livingstone, M., Hubel D. (1988). Segregation of form, color, movement, and depth: anatomy, physiology, and perception. *Science*. 1988; 240:740–749.
- Luck, S.J., and Vogel, E.K. (1997). The capacity of visual working memory for features and conjunctions. *Nature*, 390, 279-281.
- Magnussen, S., & Johnsen, T. (1986). Temporal aspects of spatial adaptation. A study of the tilt aftereffect. *Vision research*, 26(4), 661-672.
- Magnussen, S., Greenlee, M.W., and Thomas, J.P. (1996). Parallel processing in visual short-term memory. *Journal of Experimental Psychology: Human Perception and Performance*, 22, 202± 212

- Magnussen, S., Greenlee, M.W., Asplund, R., & Dyrnes, S. (1991). Stimulus-specific mechanisms of visual short-term memory. *Vision Research*, 31(7–8), 1213–1219.
- Magnussen, S. (2009). Implicit visual working memory. *Scandinavian journal of psychology*, 50(6), 535-542
- Mellet, E., Tzourio N., Denis, M., & Mazoyer, B. (1995). A positron emission tomography study of visual and mental spatial exploration. *Journal of Cognitive Neuroscience*, 4, 433–445
- Mueser KT., Bellack AS., Brady EU. (1990). Hallucinations in schizophrenia. *Acta Psychiatr Scand.* 1990;82:26–29.
- Mishkin, M., Ungerleider, LG. (1982). Contribution of striate inputs to the visuospatial functions of parieto-preoccipital cortex in monkeys. *Behav Brain Res*, 6 (1): 57–77
- Miniussi C, Ruzzoli M, Walsh V (2010). The mechanism of transcranial magnetic stimulation in cognition. *Cortex* 46: 128–130.
- Muggleton NG, Juan CH, Cowey A, Walsh V (2003) Human frontal eye fields and visual search. *J Neurophysiol* 89(6):3340-3.
- Nagarajan, S. S., Durand, D. M., and Warman, E. N. (1993). Effects of induced electric fields on finite neuronal structures: A simulation study. *IEEE Transactions on Bio-Medical Engineering*, 40 (11), 1175-88.
- Oertel, V., Rotarska-Jagiela A, van de Ven, V., Haenschel, C., Grube, M., Stangier, U., Maurer, K., and Linden D (2009). "Mental imagery vividness as a trait marker across the schizophrenia spectrum." *Psychiatry Research* 167, no. 1 (2009): 1-11.
- Pascual-Leone A, Walsh V (2001). Fast back projections from the motion to the primary visual area necessary for visual awareness. *Science* 292: 510–512
- Pasternak, T., & Greenlee, M. W. (2005). Working memory in primate sensory systems. *Nature Reviews Neuroscience*, 6(2), 97-107.
- Pearson D.G., Logie R.H., Gilhooly K.J.(1999). Verbal representations and spatial manipulation during mental synthesis. *European Journal of Cognitive Psychology*. 1999;11(3):295–314.
- Pearson D.G., Logie R.H., Green C. (1996). Mental manipulation, visual working memory, and executive processes. *Psychologische Beitrage*. 1996;38(3/4):324–342.
- Perky, C., 1910. An experimental study of imagination. *Am. J. Psychol.* 21, 422–452.
- Phillips, W. A., & Baddeley, A. D. (1971). Reaction time and short-term visual memory. *Psychonomic Science*, 22(2), 73-74.
- Phillips, W. A. (1974). On the distinction between sensory storage and short-term visual memory. *Perception & Psychophysics*, 16(2), 283-290.
- Postle, B. R., Awh, E., Jonides, J., Smith, E. E., & D'Esposito, M. (2004). The where and how of attention-based rehearsal in spatial working memory. *Cognitive Brain Research*, 20(2), 194-205.
- Postle, B. (2005). Delay-period activity in the prefrontal cortex: one function is sensory gating. *Cognitive Neuroscience, Journal of*, 17(11), 1679-1690.
- Postle, BR. (2006). Working memory as an emergent property of the mind and brain. *Neuroscience*, 139, 23-38.
- Reisberg D., Logie R.H. (1993). The ins and outs of working memory. In: Intons-Peterson M., Roskos-Ewoldsen B., Blake R., Clayton K., editors. *Imagery, creativity and discovery*. Erlbaum Associates; Hillsdale, N.J.: 1993. pp. 39–76.

- Riggall, AC., Postle, BR. (2012). The relation between working memory storage and elevated activity, as measured with functional magnetic resonance imaging. *J Neurosci* 32:12990–12998
- Repovš, G., and Baddeley, A. (2006). The multi-component model of working memory: Explorations in experimental cognitive psychology. *Neuroscience*, 139(1), 5-21.
- Romei, V., Gross, J., & Thut, G. (2012). Sounds reset rhythms of visual cortex and corresponding human visual perception. *Current biology*, 22(9), 807-813.
- Rudiak D, Marg E (1994). Finding the depth of magnetic brain stimulation: a reevaluation. *Electroenceph Clin Neurophysiol* 93: 358-371.
- Ruzzoli M, Marzi CA, Miniussi C (2010). The neural mechanisms of the effects of transcranial magnetic stimulation on perception. *J Neurophysiol* 103: 2982–2989.
- Sack, A. T., van de Ven, V. G., Etschenberg, S., Schatz, D., & Linden, D. E. (2005). Enhanced vividness of mental imagery as a trait marker of schizophrenia?. *Schizophrenia Bulletin*, 31(1), 97-104.
- Sacks O. (2010). *The Mind’s Eye*. New York: Alfred A. Knopf
- Sandrini M, Umiltà C, Rusconi E. (2011). The use of transcranial magnetic stimulation in cognitive neuroscience: a new synthesis of methodological issues. *Neurosci Biobehav Rev*. 2011 Jan;35(3):516-36
- Sakai, K., Rowe, JB., and Passingham, RE. (2002). Active maintenance in prefrontal area 46 creates distractor-resistant memory. *Nature neuroscience*, 5(5), 479-484.
- Salway AS., Logie R.H. (1995). Visuo-spatial working memory, movement control, and executive demands. *British Journal of Psychology*. 1995;86:253–269
- Segal SJ (1971) Processing of the stimulus in imagery and perception. *Imagery: Current Cognitive Approaches*: 73-100.
- Segal SJ, Fusella V (1970) Influence of imaged pictures and sounds on detection of visual and auditory signals. *Journal of experimental psychology*, 83(3p1), 458
- Segal S. J. & Nathan, S. 1964 The Perky effect: Incorporation of an external stimulus into an imagery experience under placebo and control conditions. *Perceptual and Motor Skills* 19: 385 - 395.
- Serences, JT., Ester EF., Vogel EK., Awh E. (2009). Stimulus-specific delay activity in human primary visual cortex. *Psychol Sci.*;20(2):207-14.
- Shepard R.N., Cooper L.A. MIT Press; Cambridge, MA: 1982. *Mental images and their transformations*.
- Silvanto J, Lavie N, Walsh V (2005). Double dissociation of V1 and V5/MT activity in visual awareness. *Cereb Cortex* 15: 1736–1741.
- Silvanto J, Muggleton NG (2008). New light through old windows: moving beyond the “virtual lesion” approach to transcranial magnetic stimulation. *Neuroimage* 39: 549–552.
- Silvanto J, Muggleton NG, Cowey A et al. (2007). Neural adaptation reveals state-dependent effects of transcranial magnetic stimulation. *Eur J Neurosci* 25: 1874–1881.
- Silvanto, J., Cattaneo, Z., 2010. Transcranial magnetic stimulation reveals the content of visual short-term memory in the visual cortex. *Neuroimage* 50 (4), 1683–1689.
- Silvanto, J., & Soto, D. (2012). Causal evidence for subliminal percept-to-memory interference in early visual cortex. *Neuroimage*, 59(1), 840-845.

- Slotnick, S. D. (2004). Visual memory and visual perception recruit common neural substrates. *Behavioral and Cognitive Neuroscience Reviews*, 3, 207–221
- Smith EE., Jonides, J., Koeppe, RA., Awh, E., Schumacher, EH., Minoshima, S. (1995). Spatial vs. object working memory: PET investigations. *Journal of Cognitive Neuroscience* 1995;7:337–356
- Soto, D., Wriglesworth, A., Bahrami-Balani, A., Humphreys, G.W.J., 2010. Working memory enhances visual perception: evidence from signal detection analysis. *Exp. Psychol. Learn. Mem. Cogn.* 36 (2), 441–456.
- Soto, D., Llewelyn, D., Silvanto, J., 2012. Distinct causal mechanisms of attentional guidance by working memory and repetition priming in early visual cortex. *J. Neurosci.* 32 (10), 3447–3452.
- Sparing, R., Mottaghy, F. M., Ganis, G., Thompson, W. L., Töpper, R., Kosslyn, S. M., & Pascual-Leone, A. (2002). Visual cortex excitability increases during visual mental imagery—a TMS study in healthy human subjects. *Brain research*, 938(1), 92-97.
- Sperling, G. (1960). The information available in brief visual presentations. *Psychological Monographs: General and Applied*, 74(11), 1-30.
- Sperling, G. (1963). A model for visual memory tasks. *Human Factors*, 5, 19-31.
- Sperling, G. (1967). Successive approximations to a model for short term memory. *Acta Psychologica*, 27, 285-292
- Schwarzkopf DS, Silvanto J, Rees G (2011). Stochastic resonance effects reveal the neural mechanisms of transcranial magnetic stimulation. *J Neurosci* 31: 3143–3147.
- Tolhurst, D., Thompson, P.G., 1975. Orientation illusions and after-effects. Inhibition between channels. *Vision Res.* 15, 962–972.
- Todd, JJ., Marois, R. (2004). Capacity limit of visual short-term memory in human posterior parietal cortex. *Nature*, 428(6984), 751-754.
- Todd, JJ., Marois, R. (2005). Posterior parietal cortex activity predicts individual differences in visual short-term memory capacity. *Cognitive, Affective, & Behavioral Neuroscience*, 5(2), 144-155.
- Thilo, K. V., Santoro, L., Walsh, V., & Blakemore, C. (2003). The site of saccadic suppression. *Nature neuroscience*, 7(1), 13-14.
- Thompson-Schill, SL., D’Esposito, M., and Kan, IP. (1999). Effects of repetition and competition on prefrontal activity during word generation. *Neuron*, 23, 513-522
- Tresch, MC., Sinnamon, HM., Seamon, JG. (1993). Double dissociation of spatial and object visual memory: Evidence from selective interference in intact human subjects. *Neuropsychologia* 1993;31:211–219
- Tyrrell RA, Owens DA (1988) A rapid technique to assess the resting states of the eyes and other threshold phenomena: the modified binary search (MOBS). *Behavior Research Methods, Instruments, & Computers* 20(2), 137-141.
- Ueno S, Tashiro T, Harada K (1988). Localised stimulation of neural tissues in the brain by means of a paired configuration of time varying magnetic fields. *Journal of Applied Physics* 64: 5862-5864.
- Van de Ven, V., Jacobs, C., & Sack, A. T. (2012). Topographic contribution of early visual cortex to short-term memory consolidation: a transcranial magnetic stimulation study. *The Journal of Neuroscience*, 32(1), 4-11.

- Van de Ven, V., & Sack, A. T. (2013). Transcranial magnetic stimulation of visual cortex in memory: Cortical state, interference and reactivation of visual content in memory. *Behavioural brain research*, 236, 67-77.
- Van Essen, DC. (2003). Organization of visual areas in macaque and human cerebral cortex. *The visual neurosciences*, 1, 507-21.
- Vogel, EK., Woodman, GF., and Luck, SJ. (2001). Storage of features, conjunctions and objects in visual working memory. *Journal of Experimental Psychology: Human Perception and Performance*, 27, 92-114.
- Walsh, V. and Pascual-Leone, A. (2003). *Transcranial magnetic stimulation: A neurochronometrics of mind*. MIT Press: Cambridge, MA.
- Wandell, BA. (1995). *Foundations of Vision* Sinauer Press, Sunderland, MA.
- Webster, M. A. (2011). Adaptation and visual coding. *Journal of vision*, 11(5), 3.
- Wilken, P., & Ma, WJ. (2004). A detection theory account of change detection. *Journal of Vision*, 4(12), 11.
- Wilson FW., O'Scalaidhe SP., Goldman-Rakic PS. (1993). Dissociation of object and spatial processing domains in primate prefrontal cortex. *Science* 1993;260:1955–1958.
- Wong-Riley, M. (1979). Changes in the visual system of monocularly sutured or enucleated cats demonstrable with cytochrome oxidase histochemistry. *Brain Research* 171 (1): 11–28. doi:10.1016/0006-8993(79)90728-5. PMID 223730.
- Xu, X., Ichida, JM., Allison, JD., Boyd, JD., Bonds, AB., Casagrande, V. A. (2001). A comparison of koniocellular, magnocellular and parvocellular receptive field properties in the lateral geniculate nucleus of the owl monkey (*Aotus trivirgatus*). *The Journal of Physiology*, 531(1), 203-218.
- Xu, Y. (2002a). Limitations in object-based feature encoding in visual short-term memory. *Journal of Experimental Psychology: Human Perception and Performance*, 28, 458-468.
- Xu, Y. (2002b). Integrating color and shape in visual short-term memory for objects with parts. *Perception & Psychophysics*, 64, 1260 – 1280.
- Zhang, W., and Luck, SJ. (2009). Sudden death and gradual decay in visual working memory. *Psychological Science*, 20(4), 423-428.

