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

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Abstract

Visual short-term memory (VSTM) links perception with higher cognitive processes by maintaining visual information that is absent from the environment. Yet, it remains unclear if sensory visual cortex is a necessary component of the brain network that underlies short-term maintenance of visual information. Previous reviews remain inconclusive and open to interpretation. Here, we aimed to systematically identify and review studies that have investigated the role of the sensory visual cortex in VSTM using transcranial magnetic stimulation (TMS), a method that allows exploration of causal relationships, and to quantitatively explore the effect of TMS interference on the sensory visual cortex during VSTM using meta-analytic methodology. Thirteen studies were identified and qualitatively reviewed. Out of those, seven studies provided sufficient statistical data for meta-analysis and yielded a total of 30 effect sizes, which were included in the meta-analyses. Two meta-analyses were conducted, one regarding the encoding phase of VSTM (19 effect sizes), and one regarding the maintenance phase of VSTM (11 effect sizes). The results from the systematic review and the two meta-analyses indicate that the sensory visual cortex is likely involved in both the encoding and maintenance phase of VSTM. In some cases, evidence did not show significant effects of TMS, however, this is suggested to be due to low memory load or low perceptual task demands. Overall, these findings support the idea that sensory visual areas are part of the brain network responsible for successfully maintaining information in short-term memory when no physical stimulus is present in the environment.

Keywords: primary visual cortex, early visual cortex, visual short-term memory, systematic review, meta-analysis, sensory recruitment.

Is sensory visual cortex a necessary component of the network that underlies the short-term maintenance or storage of visual information? It is well-established that visual short-term memory (VSTM) is associated with frontal (Christophel, Klink, Spitzer, Roelfsema, & Haynes, 2017; Funahashi, 2017; Levy, & Goldman-Rakic, 2000; Riley, & Constantinidis, 2016) and parietal (Bettencourt, & Xu, 2016; Ester, Sprague, & Serences, 2015; Ester, Rademaker, & Sprague, 2016; Xu, & Chun, 2006) brain areas. However, the role of the sensory visual areas (e.g., early visual areas such as V1, V2 or V5/MT+) in short-term maintenance of visual information is still unclear (e.g., Scimeca, Kiyonaga, & D'Esposito, 2018; Xu, 2017, 2020). Recent formulations of the debate focus on whether sensory visual areas are employed only during encoding of visual information (up to 200 ms after stimulus onset; Bays, Gorgoraptis, Wee, Marshall, & Husain, 2011; Brady, Störmer, & Alvarez, 2016; Kammer, 2007; Vogel, Woodman, & Luck, 2006) or if they are also engaged during the short-term maintenance of such information (Konstantinou, Bahrami, Rees, & Lavie, 2012).

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

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

Several previous attempts to reconcile disparate lines of evidence focused on qualitative reviews that lack a systematic approach of study identification, thus leaving any conclusions open to bias (Awh & Jonides, 2001; Christophel et al., 2017; D'Esposito, & Postle, 2015; Ester et al., 2016; Gayet, Paffen, & Van der Stigchel, 2018; Scimeca, Kiyonaga, & D'Esposito, 2018; Serences, 2016; Sreenivasen et al., 2014; Tapia & Beck, 2014; Teng, & Postle, 2021; van de Ven & Sack, 2013; Xu, 2017, 2018, 2020; see also Shevlin, 2020). Furthermore, most of these reviews relied heavily on neuroimaging data, which cannot provide causal information as to the question of whether the sensory visual cortex is indeed a necessary component of the network that underlies the successful short-term maintenance of visual information. (Masse et al., 2020; Serences, 2016; Sreenivasen et al., 2014; Xu, 2017; see also D'Esposito, Zarahn, & Aquirre, 1999).

In the current systematic review and meta-analyses we address these limitations by systematically identifying human studies that employed transcranial magnetic stimulation

(TMS). TMS is a non-invasive method that uses a coil to deliver magnetic pulses that can interfere with neural activity in specific brain regions with good spatial and temporal resolution (i.e., the "virtual lesion" method; Sandrini, Umiltà & Rusconi, 2011; de Graaf, & Sack, 2011; Hallett, 2000; Pascual-Leone, Walsh, & Rothwell, 2000; Pitcher, Parkin, & Walsh, 2020; Sack, 2006) and can thus furnish causal information about the relationship between brain activity and behavioral responses, as opposed to the correlational nature of neuroimaging data.

To test the hypothesis that the sensory visual cortex is a necessary component of the brain network that underlies the short-term maintenance of visual information, as suggested by the sensory recruitment hypothesis for VSTM, we performed, to the best of our knowledge, the first systematic review of the TMS literature and the first meta-analyses of this literature. Our specific aims were firstly to systematically collect and present the studies that have investigated the role of the sensory visual cortex in the encoding and maintenance of a delayed match-to-sample or a change detection VSTM task using TMS. Our second aim was to quantitively synthesize the findings of those studies using meta-analytic methods. Specifically, two meta-analyses were conducted. The aim of the first meta-analysis was to quantify the TMS effect during the encoding VSTM phase, whereas the second meta-analysis aimed to explore and quantify the presence of an effect during the maintenance VSTM phase. Additionally, small study bias was explored. Even though meta-analytic methodology is more common in clinical research, guidelines have been recently proposed for implementing meta-analyses for basic scientific questions (Mikolajewicz & Komarova, 2019).

Methods

Study selection

A systematic search of three databases (PubMed, Scopus, Web of Science) was conducted to identify relevant papers, according to published guidelines (Mikolajewicz & Komarova, 2019; Moher, Liberati, Tetzlaff, & Altman, 2009; Page et al., 2020). Since this was the first attempt to systematically gather such evidence, the search was conducted without chronological limitations and applied within all fields of the databases. Three of the authors (PP, AT, NK) designed and completed the search strategy.

The literature search ended in January 2021. Initially, data were extracted by a literature search that was conducted in June 2020. The literature search was repeated in January 2021, however no additional studies were identified to be included in the systematic

review and meta-analyses. Details of the final literature search are presented using a PRISMA flow diagram in Figure 1. The literature search was conducted using the following thread: ((("visual short term memory" OR "vstm" OR "visual working memory" OR "short term memory" OR "working memory")) AND ("primary visual cortex" OR "sensory recruitment" OR "sensory recruitment hypothesis" OR "early sensory cortex" OR "early visual cortex")) AND ("transcranial magnetic stimulation" OR "tms" OR "behavioural" OR "behavioral" OR "brain stimulation" OR "visual mask" OR "manipulation" OR "reaction time" OR "reaction times" OR "accuracy"). Additionally, studies were identified through previous review papers (Awh & Jonides, 2001; Christophel et al., 2017; D'Esposito, & Postle, 2015; Serences, 2016; Sreenivasen et al., 2014; Tapia & Beck, 2014; van de Ven & Sack, 2013; Xu, 2017, 2020). Two of the authors (PP and AT) independently assessed the reports that derived from the initial search, based on predetermined inclusion and exclusion criteria (see below). In the case where consensus was not reached between the two, the author NK independently assessed the ambiguous report and group discussions were held to reach a final agreement.

Following the PRISMA statement (Moher et al., 2009) for systematic reviews and meta-analyses, 13 articles matched the criteria and were included in the systematic review. Of these 13 articles, six provided sufficient statistical data to estimate effect sizes and thus be included in the meta-analyses (see Figure 1). The corresponding authors of the remaining papers were contacted through email and further data were requested in order to compute effect sizes and therefore make the studies eligible for the quantitative analysis of this review. One author responded by providing additional data and thus making the final number of included studies in the meta-analyses seven.

Inclusion and exclusion criteria

To identify papers eligible for the systematic review, three inclusion criteria were determined, which comprised of: (1) behavioural measures of VSTM performance (i.e., accuracy, absolute error, percent correct, precision, guess rate and signal detection), (2) causal interference of the sensory visual cortex using TMS during a VSTM task, and (3) human participants. In addition, two exclusion criteria were defined which included: (1) any form of mental or physical pathology and (2) reports written in a language other than English. No age limitations were set for our search, however the identified studies solely included adults. In order for the studies to be further included in the meta-analyses, they further had to provide arithmetic data (means and SDs or t scores) on behavioral performance scores during a VSTM task in a TMS interference condition and at least one control condition. These

variables varied according to study design (i.e., different measures for match-to-sample tasks than for change-detection tasks) and included measurements of accuracy, absolute error, percent correct, precision, guess rate and signal detection (*A'*).

Data Analysis

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

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

Given the methodological differences found in TMS studies (see de Graaf, & Sack, 2011), significant heterogeneity, tested with the I^2 index, was expected between the studies (van de Ven & Sack, 2013). According to Higgins, Thompson, Deeks, and Altman (2003), the I^2 index levels can be described as low, moderate, and high, when they fall close to 25%, 50%, and 75%, respectively. We estimated effect sizes for each individual data set using the Hedge's *g* (Hedges, 1981) formula. The effects sizes were then pooled using a random-effects model (Fleiss, 1993).

Data analysis was conducted using R (v4.0.2) and RStudio (v1.1.456) (R Core Team, 2020; see also Harrer, Cuijpers, Furukawa, & Ebert, 2019). Hedge's *g* (Hedges, 1981) effect sizes were calculated using the esc library (Lüdecke, 2018). The effect sizes were pooled using a random effects model (Fleiss, 1993) using the meta package for R (Schwarzer, 2007). Specifically, the meta-analyses were conducted using the inverse variance method, where variance includes both within- and between-study variance. The maximum-likelihood estimator was used for tau^2 and the *Q*-profile method was used for the tau and tau^2 confidence intervals. Forest plots were used for data visualization. Due to the small number of studies included in the meta-analyses, moderator variables analysis was not possible to conduct. To test for small study bias, funnel plots were generated to visually investigate their symmetry which was further examined using the Egger's test (Egger, Smith, Schneider, & Minder, 1997).

Some individuals participated in more than one experiment and/or experimental condition. Because this violates the independency of some data points, we performed two

three-level meta-analyses (one for each meta-analysis; see Assink & Wibbelink, 2016; Cheung, 2014; Pastor & Lazowski, 2018). We included an additional level in the meta-analyses, referred here as the study level, where we clustered each experiment and/or experimental condition to its corresponding study. This analysis allowed us to explore how the different levels explain variance in the model. We then repeated the analyses excluding the study level and compared the fitness of the two-level and three-level models.

Data availability statement

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

Results

The systematic search of the literature led to the identification of 13 papers. These papers included a total of 17 experiments that interfered with sensory visual cortex activity using TMS during a VSTM task. A total of 228 individuals participated in the 17 experiments (*mean age*=12.35 yrs, *sd*=3.71). Short descriptions of the included studies and their experiments are presented in Table 1.

Systematic Review

Methodological Issues. A number of methodological issues such as the different apparatuses used (i.e., stimulator, coil), targeting methods (e.g., neuronavigation, phosphene induction), as well as the different output settings (e.g., power, frequency, number of pulses) have been identified (de Graaf, & Sack, 2011; Pitcher, et al., 2020; Sadrini, et al., 2011) as factors that can possibly affect the homogeneity of the experiments (van de Ven & Sack, 2013). In the studies considered here, TMS stimulation was delivered with a 70 mm figure-of-eight coil in all experiments. The majority of experiments ($n = 15$) targeted area V1, while two focused on V5/MT+. Seven of the included experiments aimed to directly investigate the role of the sensory visual cortex in VSTM. The remaining six studies had different aims, but nevertheless reported behavioural outcomes whilst interfering with TMS on the sensory visual cortex during a VSTM task, making them useful for the purposes of this systematic review and meta-analysis. In eight of the included experiments, TMS output power was determined using the functional method of eliciting phosphenes (see Walsh, & Pascual-Leone, 2003), while in the remaining nine a fixed TMS power output was used. When interfering with the sensory visual cortex, two experiments delivered TMS in four pulses, three in five pulses, six delivered three-pulse TMS, and six experiments delivered a single

TMS pulse. Moreover, seven experiments targeted the sensory visual cortex in only one hemisphere.

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

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

TMS interference during encoding. The effects of TMS interference of the sensory visual cortex activity during the encoding phase of visual information was tested in six experiments, from five studies (Cattaneo, Vecchi, Pascual-Leone, & Silvanto, 2009; Koivisto, Harjuniemi, Railo, Salminen-Vaparanta, & Revonsuo, 2017; Rademaker, van de Ven, Tong, & Sack, 2017; van de Ven, Jacobs, & Sack, 2012; van Lamsweerde, & Johnson, 2017). As expected, the majority of these studies presented evidence supporting the involvement of the sensory visual cortex during VSTM encoding.

Cattaneo et al. (2009) used TMS to interfere with sensory visual cortex during a visual imagery task or a VSTM task. Participants were presented for 1 second with either an

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

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

Koivisto et al. (2017) provided evidence supporting the involvement of the sensory visual cortex during VSTM encoding through their paradigm, even though their research objectives differed from the ones of this systematic review. Following these sensitive statistical methods, some studies, which directly investigated the role of the sensory visual cortex during VSTM encoding, provide additional support for its involvement. Rademaker et al. (2017) asked participants to match the orientation of one out of four gratings which were presented for 200 ms in four visual field quadrants corresponding to either the same, ipsilateral, contralateral, or diagonal TMS ROI. TMS was delivered either at the beginning (0 ms after stimulus onset) or midway during a 2 second delay period (900 ms, see section *TMS*

interference during maintenance for further details) of the VSTM task and a sham TMS condition was also used as control. The authors reported more errors when stimulation matched the remembered-item location compared to when the remember-item location was furthest to the stimulation. Also, early stimulation had a significantly stronger effect compared to late stimulation. Additionally, higher precision was measured when the pulse and target overlapped (same and ipsilateral conditions) compared to when they were far apart (diagonal condition) and guessing was reported higher when TMS was earlier than later.

Similarly, participants in an experiment by van Lamsweerde and Johnson (2017) had to remember the color of three squares presented for 150 ms. A probe presented after a 1 second delay period asked them to match the color of one of the three remembered squares. During the VSTM task, TMS was induced at 0, 100, or 200 ms after stimulus offset. Results indicated that guess rates were higher in the TMS contralateral condition, especially at stimulus onset. Further, a significant interaction of TMS and side (ipsilateral/contralateral) was reported on precision, with the effect seeming stronger at the 100 ms condition. Swap rate effects (an indication of recalling a non-cued item) were also reported, which were significantly decreased in the contralateral compared to the ipsilateral condition. Given the stronger effects at the 0 ms and 100 ms timings, similar to Koivisto et al. (2017) described above, the authors concluded that TMS effects are evident during memory encoding, but are no longer affective once consolidation has been achieved at 200 ms.

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

However, the lack of an effect in the 100 ms condition could be due to a number of methodological issues. Specifically, van de Ven et al. (2012) used two different localisation methods and found a significant difference in the variable of interest (significantly different

A' under the higher load condition of their experiment, which was the only condition reported to have significant results) between the participants depending on which localisation method group they belonged to. Furthermore, since comparisons were made between the memory load condition and the TMS timing, it is likely that a TMS effect actually does exist in both conditions (i.e., TMS affected memory performance in both load conditions). For example, no additional control condition (e.g., sham or no TMS) was used other than the ipsilateral visual hemifield of the targeted ROI. Therefore, given the lack of dichoptic stimulus presentation (see Carmel, Arcaro, Kastner, & Hasson, 2010), it remains possible that encoding of the visual information was in fact processed by the sensory visual cortex in both hemispheres (Tong, Meng, & Blake, 2006) and thus the effect remained undetected when comparing the ipsilateral versus the contralateral condition of the experiment. Additionally, the lack of effect in the 100 ms condition could be due to a lack of TMS interference or perhaps due to the fact that the stimulus remained visible for an additional 50 ms following TMS interference, thus allowing participants to successfully encode the stimulus despite TMS interference.

In summary, the findings of the studies described above indicate that, apart from the experiment reported by van de Ven et al. (2012), all five remaining experiments reported a TMS effect on behavioral performance during the encoding phase of a VSTM task indicating that the results from studies using TMS to interfere with the sensory visual cortex during the encoding phase of VSTM are consistent with the well-established role of the sensory visual cortex in VSTM encoding.

Next, we turn to the evidence from human TMS studies examining the involvement of sensory visual cortex in short-term maintenance.

TMS interference during maintenance. TMS was delivered during the maintenance phase of a VSTM task (i.e., more than 200 ms after stimulus onset) in 12 experiments from ten different studies (Cattaneo, Bona, & Silvanto, 2012; Malik, Dessing, & Crawford, 2015; Rademaker et al., 2017; Saad, & Silvanto, 2013; Saad, Wojciechowska, & Silvanto, 2015; Silvanto & Cattaneo, 2010; Silvanto, & Soto, 2012; Soto, Dlewelyn, & Silvanto, 2012; van de Ven et al., 2012; Zokaei, Manohar, Husain, & Feredoes, 2014). As discussed in detail below, although the majority of these studies provide evidence supporting the sensory recruitment hypothesis, others either failed to find such evidence or their findings are more consistent with an interaction between perceptual and VSTM processes.

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

The involvement of area V5/MT+ in VSTM maintenance was further supported in two experiments by Zokaei et al. (2014). In the first experiment participants were asked to remember two motion stimuli presented above and below fixation for 200 ms. The color of each stimulus was either red or green and one color was probed. Participants had to match the movement direction of the remembered stimulus to that of the probe. During the 3.7 second delay period of this task, participants were also asked to identify, after being probed with a color, if the same-colored stimulus was above or below fixation. After 3.2 seconds into the delay period, TMS was delivered, followed by the memory probe. In the second experiment, the two motion stimuli, instead of being presented together, were sequentially presented for

300 ms each and each was followed by a 1 second delay period. TMS was applied 300 ms after the onset of either the first or the second stimulus. Following the second stimulus, a colored probe appeared indicating to participants to match its direction to that of the same-colored motion stimulus's direction. A low intensity TMS condition was used in both experiments as a control condition and a vertex TMS condition was additionally introduced in the second experiment. The results of the first experiment showed that in the ineffective TMS condition there was a significant impairment in performance between congruent (if the position identification task probe matched the color of the memory task probe) and incongruent (if the position identification task probe did not match the color of the memory task probe) conditions which disappeared in the effective TMS condition. Similarly, in the second experiment, a significant impairment in precision was found in the low TMS condition when the first stimulus was followed by TMS, compared to when the second stimulus was followed by TMS; this effect was not evident in the high TMS condition. The authors described this as a facilitation effect of TMS, explaining that non-privileged memory items (i.e., memories in the incongruent trials; see Hitch, Allen, & Baddeley, 2020) were likely suppressed and thus enhanced by stimulation. Since TMS can enhance neural excitability, in addition to inhibiting brain processing (Robertson, Theoret, & Pascual-Leone, 2003), this facilitation effect is consistent with the findings of Silvanto and Cattaneo (2010) suggesting the involvement of area V5/MT+ during VSTM maintenance.

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

        Additional evidence for the role of areas V1/V2 was found by van de Ven et al. (2012) (also described above in the section *TMS interference during encoding*), during

sensory visual cortex stimulation in two different conditions throughout the 1.5 second delay period, at 200 ms and 400 ms after stimulus onset (as well as at 100 ms corresponding to encoding; discussed in the previous section). TMS affected task performance in the contralateral compared to the ipsilateral condition only in the high load 200 ms TMS condition. These findings support the involvement of the sensory visual cortex in the maintenance of visual information, mainly during the 200 ms window. Likewise, in Rademaker et al.'s (2017) study (also described previously; see TMS interference *during encoding* section), the sensory visual cortex was stimulated 900 ms into the delay period of their VSTM task. As discussed previously, more errors were reported when stimulation matched the remembered-item location compared to when the remember-item location was furthest to the stimulation and higher precision was reported when TMS and target overlapped (same and ipsilateral conditions) compared to when they were further apart (diagonal condition). Taken together these results indicated that stimulation that overlapped with the same or ipsilateral visual field affected task performance when compared to the visual field that was further apart. However, it should be noted that these results were larger for earlier (during encoding) rather than later (during maintenance) stimulation.

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

In a similar manner, an interaction between perception and memory processes was discussed by Saad et al. (2015), who investigated the differences between imagery and VSTM neural bases. In their VSTM condition, participants had to memorize the contrast of a grating presented for 300 ms throughout a 4 second delay period. Sensory visual cortex TMS

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

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

an interaction of TMS with perceptual processes, modulated by what is maintained in memory.

Similar results were found in a group of experiments by Saad et al. (2013), where they examined how the tilt aftereffect can affect memory representations. In two of their experiments, sensory visual cortex TMS was applied during a VSTM task. In the VSTM condition of the first experiment participants were requested to remember the orientation of a grating and in the second experiment the color and size of one square. In both cases, the memory sample was presented for 300 ms and was maintained during a 5.3 second delay period, which was followed by a same-sized adapter grating, that had either the same or a 20-degree tilt difference (in the same direction) from the memory sample. In the first experiment, TMS was delivered either at 2 or 5 seconds into the delay period. In the second experiment, TMS was delivered only at 2 seconds into the delay period. In the VSTM conditions, a probe appeared after the delay period where participants had to report the change from the memory sample (first experiment) or match it to the memory sample (second experiment). Results showed no difference between TMS and a sham TMS control condition on the memory task, however the tilt aftereffect, was significantly decreased by TMS in the memory condition (compared to a passive one). Similarly to the results of Soto and Silvanto (2012), the tilt aftereffect, which is a perceptual process, was modulated by memory requirements, indicating once more an interaction between perceptual and memory processes.

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

The majority of the TMS studies investigating the involvement of the sensory visual cortex during VSTM maintenance reported evidence supporting the sensory recruitment hypothesis. However, four experiments described in three different papers reported no direct

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

This interaction between perceptual and memory mechanisms, as well as the role of processing load, have been identified and reported in other sensory visual cortex TMS studies (Saad et al., 2015; Silvanto & Soto, 2012; van de Ven et al., 2012). This interaction has also been supported by behavioural studies, which suggested that the perception of visual stimuli and VSTM are underlaid by shared neural mechanisms (Magnussen, Greenlee, Asplund, & Dyrnes, 1991; McKeefry, Burton, & Vakrou, 2007). Furthermore, the VSTM load and perceptual performance relationship has been previously studied, indicating that VSTM capacity load can affect both performance and sensory visual cortex activity (Konstantinou, et al., 2012; Konstantinou, Beal, King, & Lavie, 2014; Konstantinou, & Lavie, 2013). In fact, the sensory recruitment hypothesis stems from this shared neural substrate between perception and VSTM (Pasternak, & Greenlee, 2005), which is reflected in dual and distraction tasks (for a recent review see Lorenc et al., 2021). Thus, a possible explanation for the failure to detect a TMS effect in these experiments is low sensory visual cortex neural demands (i.e., perceptual and/or memory load). For example, studies have indicated that the maximum number of visual objects that can be maintained in VSTM is estimated to range between three and four items (Cowan et al., 2005; Luck, & Vogel, 1997; Todd, & Marois, 2004; Vogel, et al, 2001, 2005; Vogel, & Machizawa, 2004). Therefore, if this is reflected in the sensory visual cortex's activity, it is possible that enough resources were still available in

the sensory visual cortex due to low load VSTM task demands, thus, TMS noise leaves the maintained representations unaffected (see de Graaf, & Sack, 2011).

Taken together, the results from the systematic review on TMS interference during memory maintenance indicate that the sensory visual cortex is likely involved in VSTM maintenance, supporting the sensory recruitment hypothesis. This is reflected in all but one studies by the direct TMS effects on memory performance and the TMS interaction effect between perception and VSTM. Next we turn to a quantitative analysis of these results using meta-analytic methodology in order to statistically test these conclusions.

Meta-Analysis

Meta-analysis 1: TMS interference during encoding. Five studies totaling $n = 229$ participants were included in the meta-analysis investigating the effect of TMS during the encoding of visual information. Out of these five studies, a total of 19 effect sizes were calculated based on all the relevant experimental conditions. All effect sizes are presented in Table 2.

As expected, heterogeneity was significant amongst data sets, $Q(18) = 90.20$, $p < .0001$, with high inconsistency between studies, $I^2 = 80\%$, $\tau^2 = 1.16$, 95% $CI = .61, 3.37$. We proceeded with a random effects model which provided a significant standardized difference in means of $d = .74$, 95% $CI = .20, 1.28$, $Z = 2.70$, $p = .007$, indicating that TMS during encoding on the sensory visual cortex does have an effect on VSTM behavioural outcomes. The forest plot of the meta-analysis during encoding is illustrated in Figure 2A.

Further, small study bias was investigated using visual inspection of a generated funnel plot (see Figure 2B) and using the Egger's Test. The right side of the inverted funnel is underrepresented, indicating that more studies showing a stronger TMS interference effect in VSTM encoding are needed to make the funnel symmetrical. Both approaches indicated possible small study bias, given the asymmetry of the funnel plot and a significant Egger's Test, *intercept* $= 10.31$, $t(18) = 5.73$, $p < .001$.

The three-level meta-analysis indicated that no variance was explained by the study level, $\sigma^2 = 0$, total $I^2 = 76.57\%$ (see Figure 3). An analysis of variance comparison of the two-level model ($df = 2$, $AIC = 44.34$, $BIC = 46.12$) and the three-level model ($df = 3$, $AIC = 46.34$, $BIC = 49$) showed no significant differences between them ($p = 1$). Since no variance was explained by the study level, and no significant difference was found between the two-level and three-level models it is not likely that our meta-analysis results were affected by dependent effect sizes' correlations.

Meta-analysis 2: TMS interference during maintenance. A total of five studies totaling $n =$ 145 participants were included in the meta-analysis of the effect of TMS during the maintenance of visual information. From the relevant experimental conditions of these five studies, a total of 11 effect sizes were calculated. The effect sizes are presented in Table 3.

Heterogeneity was significant amongst data sets, $Q(10) = 22.12$, $p = .014$, with moderate inconsistency between studies, $I^2 = 54.80\%$, $\tau^2 = 0.22$, 95% $CI = .02, 1.29$. The random effects model provided a significant standardized difference in means of $d = .47$, 95% $CI = .07, .87$, $Z = 2.31$, $p = .021$, providing evidence that TMS applied on the sensory visual cortex during the maintenance phase of a VSTM task results in a significant difference on VSTM behavioural outcomes. The forest plot of the second meta-analysis is shown in Figure 4A.

As previously, small study bias was investigated by visually inspecting a generated funnel plot (see Figure 4B) and with the Egger's Test. Once again, publication bias was evident both in the asymmetry of the funnel plot and a significant Egger's Test, *intercept* = 5.91, $t(10) = 4.24$, $p = .002$.

No variance was explained by the study level, $\sigma^2 = 0$, total $I^2 = 39.59\%$ according to the three-level meta-analysis (see Figure 5). The two-level model (*df* = 2, *AIC* = 22.67, *BIC* = 23.28) and the three-level model (*df* = 3, *AIC* = 24.67, *BIC* = 25.58), when compared using analysis of variance, showed no significant differences between them ($p = 1$). The lack of explained variance by the study level, combined with the lack of a difference between the two-level and three-level models, shows that our meta-analysis results were not likely affected by correlations form dependent effect sizes.

Discussion

A systematic review and two meta-analyses were conducted to investigate whether the sensory visual cortex is part of the brain network responsible for the encoding as well as the short-term maintenance of visual information. We focused on studies that interfered with sensory visual cortex using TMS during the encoding and maintenance phases of VSTM. The systematic review identified 13 papers that included 17 experiments and totaling 228 participants. Two meta-analyses were performed using the subset of studies that provided sufficient data for behavioral measure scores for a TMS and a control condition. The meta-analyses investigated separately the role of the sensory visual cortex in encoding and short-term maintenance of visual information. The findings indicate that encoding and maintaining

visual information in VSTM are both supported by a brain network that includes sensory visual cortex.

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

Previous neuroscientific evidence produced with various methodological approaches (e.g., Bettencourt, & Xu, 2016; Lee et al., 2016; Lu et al., 2018; Tcheslavski et al., 2018) together with the findings of the present systematic review and meta-analysis 1, establish the involvement of the sensory visual cortex in encoding of visual information in VSTM. Here, we extend this previous evidence to now include evidence from studies that employed TMS. Moreover, replicating the well-established finding of the causal involvement of sensory visual cortex in encoding of visual information in VSTM provides further evidence for the validity of TMS in indeed being a suitable method to provide causal evidence in the form of a "virtual lesion" that disrupts neural activity subserving cognitive processing involved in encoding as well as maintenance of visual information in VSTM, as we discuss next.

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

sensory recruitment hypothesis and our main findings (Pasternak, & Greenlee, 2005; see also Lorenc, et al., 2021).

Overall, the present systematic review and meta-analyses point to the direction of an involvement of the visual sensory cortex, not merely in the encoding, but also in the maintenance of visual information. Our findings are not in agreement with recent reviews, which suggest that there is insufficient evidence to support the sensory recruitment hypothesis (Xu, 2017, 2020). However, these reviews were heavily reliant on neuroimaging studies that are not suitable for detecting activity silent mechanisms thus ignoring any potential involvement of sensory visual cortex during memory maintenance (Masse et al., 2020; Oberauer, 2019; Rose et al., 2016; Serences, 2016; Sreenivasen et al., 2014). Additionally, the activity-silent processes of the sensory visual cortex have been generating a lot of still unanswered questions, such as the one raised by Oberauer (2019) about whether neurally active representations are actually functionally important for maintaining information in working memory. To address these issues, we focused on studies using TMS for disrupting content-specific neural activity, thus providing causal evidence on the cognitive process subserved by activity of the brain area being targeted by TMS (de Graaf et al., 2014; Pitcher, et al., 2021; Sadrini, et al., 2011; Tapia & Beck, 2014; van de Ven & Sack, 2013). An additional explanation of the different conclusions between our study and those previous reports is the fact that many of the experiments identified here that showed an interference of TMS with the sensory visual cortex during the VSTM maintenance phase were not included in those reviews. This omission on behalf of the previous reviews showcases the importance of systematically searching the literature by following established guidelines (e.g., Moher et al., 2009, Page et al., 2020).

Our findings help clarify why previous reports (e.g., Xu, 2017, 2018, 2020) suggest that any possible involvement of the sensory visual cortex during short-term maintenance is most likely a result of feedback from higher brain areas, such as the prefrontal and posterior parietal cortex. This suggestion was based on neuroimaging data showing that VSTM representations in the sensory visual cortex were wiped out at no behavioral cost, after task-irrelevant distractors were presented in a delayed match-to-sample (Bettencourt & Xu, 2016; but see Rademaker et al., 2019 for a different result that is in line with the findings reported here). However, considering the flexibility of the working memory system, where information can be transferred through interactions between sensory and frontal areas (Christophel et al., 2017; D'Esposito & Postle, 2015), this argument remains compatible with the idea that the sensory cortex is a necessary component of the network that underlies short-

term maintenance of visual information (Gayet et al., 2018; Scimeca et al., 2018). These interactions are vital for memory maintenance in the sensory visual cortex and for other attentional processes (D'Esposito, 2007; D'Esposito & Postle, 2015), meaning that activity in the frontal brain areas does not exclude or makes redundant the involvement of the sensory visual cortex during memory maintenance but rather highlight that the successful short-term maintenance of visual information relies on a network of brain areas instead of activity of isolated brain areas.

An alternative explanation for the effects of TMS on memory performance reported here is that TMS does not interfere directly with the maintenance processes, but these effects reflect instead an interruption of attentional processes. For example, research suggests that sensory cortices are mediated by attentional mechanisms that synchronize neural oscillations (Bauer, Debener, & Nobre, 2020). Recently, it was shown that TMS induced in different frequencies can affect VSTM performance accordingly (Riddle, Scimeca, Cellier, Dhanani, & D'Esposito, 2020). Yet, recent research provides evidence that working memory seems to similarly rely on phase-dependent oscillations (ten Oever, De Weerd, & Sack, 2020). Future research on phase-dependent cognitive mechanisms could possibly provide explanations relevant to the sensory recruitment hypothesis. For instance, future work could unveil if attention and working memory depend on the same oscillation phase (e.g., Arnulfo, et al., 2020; Li, et al., 2020) or if different frequency patterns explain each mechanism.

A limitation of the current study is the heterogeneity between the identified studies. Such heterogeneity was expected given the different methodological approaches, especially regarding the different parameters of stimulation using TMS (de Graaf, & Sack, 2011; Pitcher, et al., 2021; Sadrini, et al., 2011; van de Ven & Sack, 2013). Yet, this significant heterogeneity raises some important issues that ought to be discussed and addressed. Given the active debate around the sensory recruitment hypothesis and the different interpretation of the current literature (Ester et al., 2016; Gayet, Paffen, & Van der Stigchel, 2018; Scimeca, et al., 2018; Shevlin, 2020; Teng, & Postle, 2021; Xu, 2018), it is fundamental to focus on reproducible practices. Specifically, future studies should focus on specific methodological and technical approaches, in such a manner that between study comparisons, both qualitatively and quantitatively, can be more accurately implemented (see Hardy, & Thompson, 1998; Higgins, & Thompson, 2002; Pitcher, et al., 2021). For example, future studies should aim to report all relevant results, given that even null results in TMS studies are often informative and important (de Graaf, & Sack, 2011). One way of promoting this, is by preregistering experiments (see Nosek, Ebersole, DeHaven, & Mellor, 2018) and by

uploading the raw data sets in open repositories, such as osf.io. It is also suggested that future studies offer sufficient information regarding TMS parameters (e.g., localization, power output, coil position, frequency) in a manner which will guide and promote reproducibility (see Peterchev et al., 2012). Further, TMS studies in the field of cognitive neuroscience should carefully design their experiments (e.g., use more than one control condition) in order to produce more reliable results (Pitcher, et al., 2021; Sadrini, et al., 2011).

Another important issue that needs to be raised is the dependency of the calculated effect sizes. Given that some individuals participated in more than one experiment and since in some cases more than one effect size was calculated for some of the included studies in the meta-analyses, it is possible that some effect sizes are biased, since they are not independent (Cheung, 2019). Nevertheless, given the small number of available datasets we proceeded with the most conservative approach to our meta-analyses, namely the random effect model. In order to explore if the dependency of some of the data could account for our results, we clustered each experimental condition to its corresponding study, thus creating an additional level in each of our meta-analysis models. This additional study level could not explain the variance in our meta-analyses models indicating that the results were likely not affected by correlations in the dependent effect sizes.

Significant small study bias was identified, which was reflected in the asymmetry of the funnel plots and the significant statistical tests for small study bias in both meta-analyses. This could indicate a possible publication bias, often referred to as the file drawer problem (e.g. Nagarajan, Garla, Taranath, & Nagarajan, 2017; see also Friese, & Frankenbach, 2019), which has been shown to be common in cognitive neuroscience (Huber, Potter, & Huszar, 2019). However, by considering the fact that almost half of the identified studies explored a different research question, in addition to the small number of identified studies, no robust conclusions regarding this kind of bias can be drawn. Although, it must be noted that publication bias can affect the results of the meta-analysis both for the Q test, as well as the heterogeneity test by increasing or decreasing the value of the true effect sizes (Augusteijn, van Aert, & van Assen, 2019; Friese, & Frankenbach, 2019). In general, to reduce bias scientists and journals should be encouraged to publish with a focus on robust scientific methodology as opposed to whether results are significant or not.

In summary, evidence from studies that interfered with sensory visual cortex activity using TMS during VSTM, support the involvement of the sensory visual cortex in VSTM encoding as well as VSTM maintenance. Interestingly, TMS in low VSTM load conditions is not as effective as with higher load, and similarly, increased perceptual demands can

modulate TMS effects. Given the importance of reproducible practices, it is suggested that the specific parameters of stimulation using TMS are carefully implemented, which will encourage future and more robust systematic and meta-analytic approaches to cognitive science.

Conclusion

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

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Figures and Tables

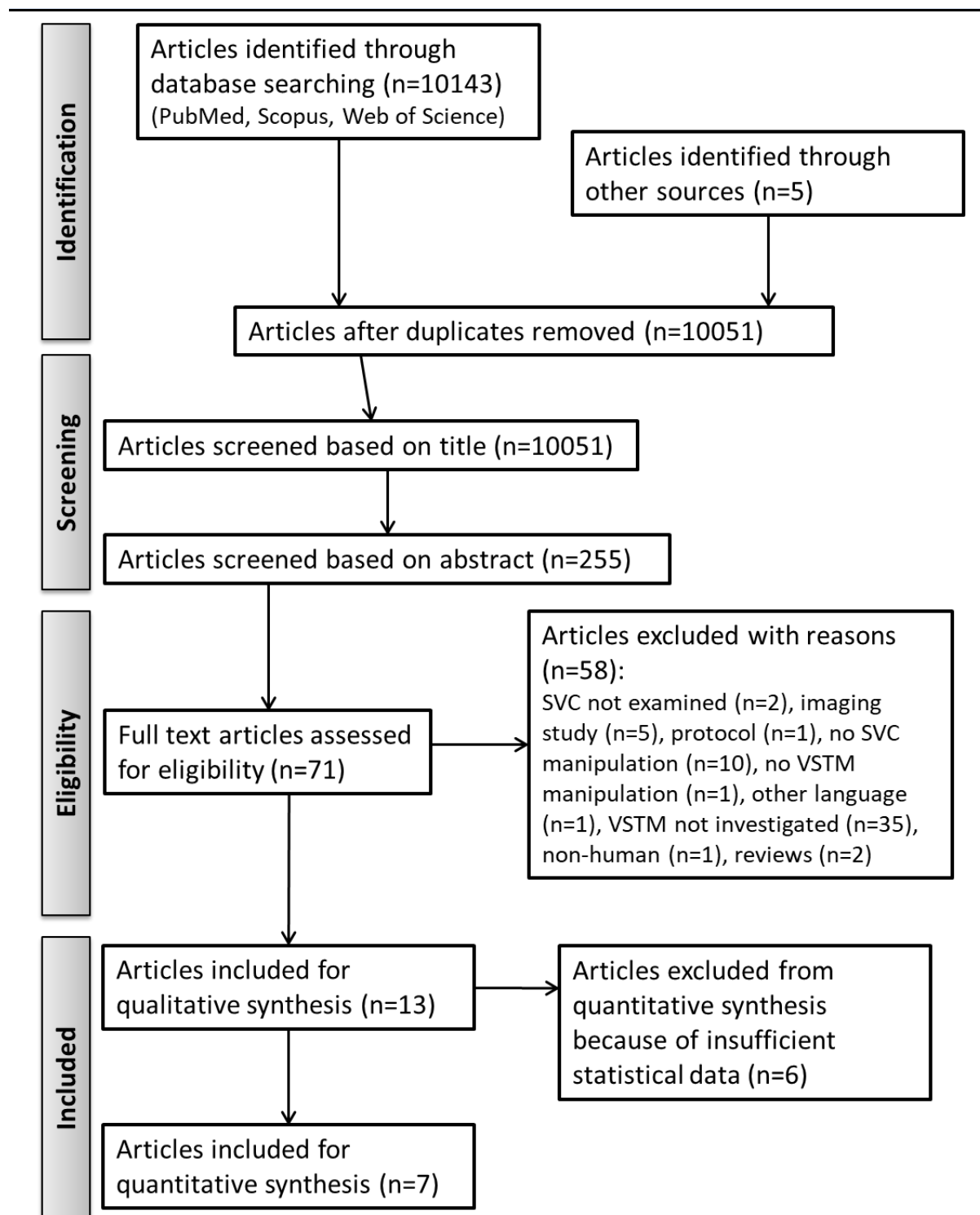**Figure 1:** The study's PRISMA statement.

Fig 1. The PRISMA flow diagram followed for the systematic review and meta-analyses as suggested by Moher et al. (2009). Screening and eligibility assessment were completed by two independent researchers. SVC; sensory visual cortex, VSTM; visual short-term memory.

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

	ARTICLE	DESCRIPTION	ROI (PULSE)	TARGETING (OUTPUT POWER)	TASK	CONTROL	TMS TEMPORAL POINT (AFTER STIMULUS OFFSET)	N	BEHAVIOURAL MEASURE
1	Cattaneo et al. (2009)	SVC role in mental-imagery and short-term memory	V1 (sp)	Phosphene induction (65% of Magstim 200 stimulator)	Time Memory or imagery task	No TMS & vertex TMS	**Exp1:** 2000 ms **Exp2:** 0 ms	**Exp1**: 14 **Exp2:** 14	Accuracy
2	Silvanto et al. (2010)	SVC role in VSTM	Right or left V5/MT+ (sp)	Phosphene induction (120% of phosphene threshold)	**Exp1:** motion speed detection task	Ipsi-/contra- & No TMS	3000 ms	12	Accuracy
3	Cattaneo et al. (2012)	SVC role in mental imagery	V1 (3p)	2cm above inion (60% of Magstim SuperRapid stimulator)	**Exp2:** Time imagery task	No TMS & vertex TMS	1000 ms	10	Accuracy
4	Soto et al. (2012)	SVC role in attentional guidance by priming and working memory	V1 (3p)	2cm above inion (90% of phosphene threshold)	Priming detection task, with working memory task	Sham TMS	1700 ms	12	Accuracy
5	Silvanto et al. (2012)	Subliminal perception interference in memory	V1 (3p)	Phosphene induction (90% of phosphene threshold for n=7, 50% of Medtronic MagPro R 30 stimulator for n=3)	**Exp1b:** Orientation change detection task	Sham TMS	1000 ms	**Exp1b**: 10	Detection sensitivity
6	van de Ven et al. (2012)	SVC role in VSTM	Right or left V1 (sp)	(1) Phosphene induction for n=8 (2) Neuronavigation for n=5 (110% of phosphene threshold)	**Exp2:** Non-natural shape change-detection task	Ipsi-/contra-	100 ms, 200 ms or 400 ms	13	Detection sensitivity
7	Saad et al. (2013)	Effects of external visual input in internal representations	V1 (5p)	2cm above and .5cm laterally from the inion towards the right hemisphere (45% of a Nexstim stimulator)	**Exp2:** Orientation change detection task **Exp3:** Shape change detection task	Sham TMS	**Exp2:** 2000 ms or 5000 ms **Exp3:** 2000 ms	**Exp2:** 16 **Exp3:** 8	Accuracy

Table 1 Continued

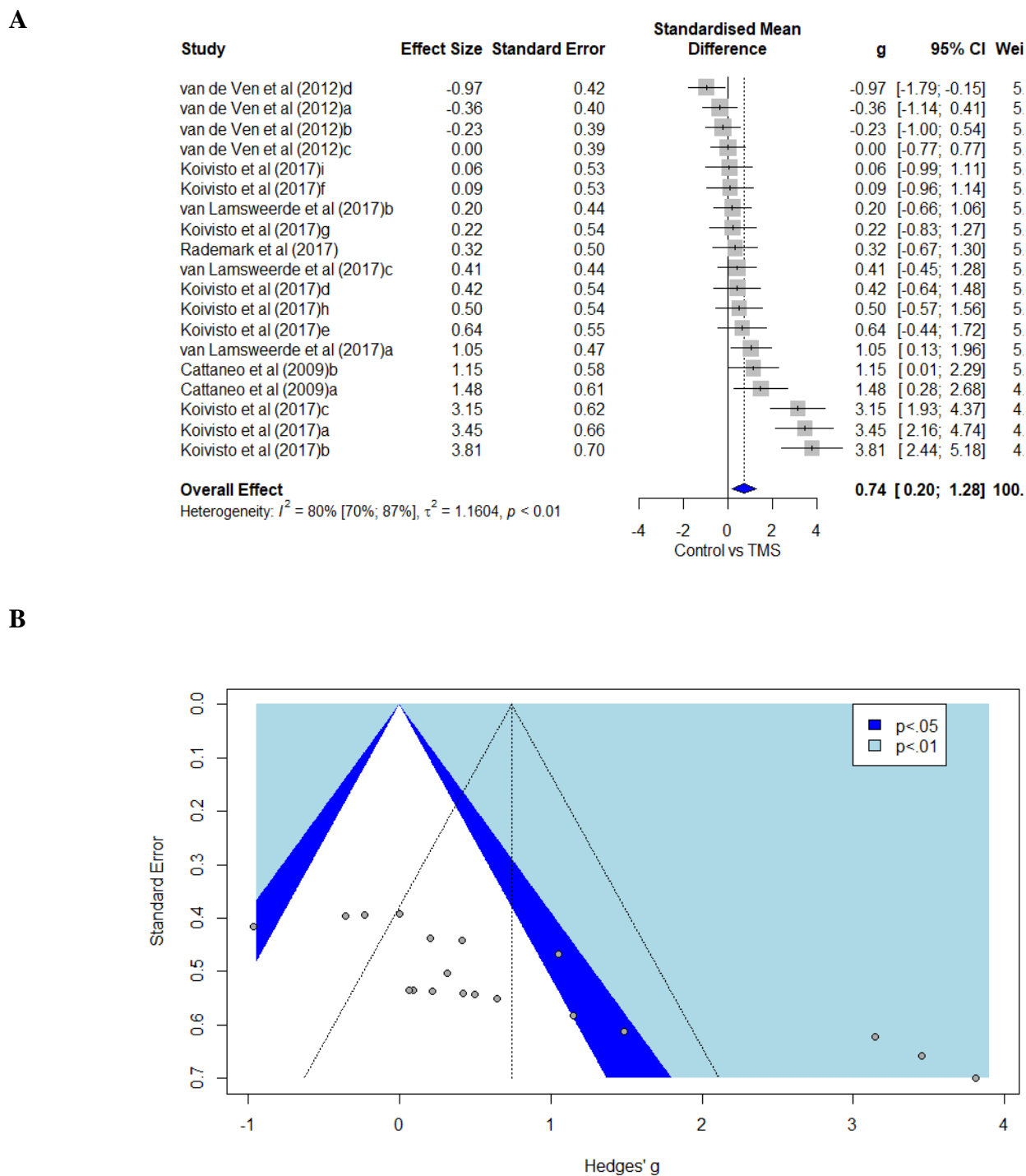|									
8	Zokaei et al. (2014)	Effects of TMS depending on representation state in VSTM	V5/MT+ (4p)	fMRI localization (60% of Magstim Rapid^2 stimulator)	Motion match to sample task	**Exp1:** low power TMS **Epx2:** Low power TMS & Vertex TMS	**Exp1:** 3100 ms **Exp2:** 300 ms after first or second memory array	**Exp1:** 13 **Exp2:** 17	Precision
9	Malik et al. (2015)	SVC role in trans-saccadic memory of features	Right and left V1 (3p)	Neuronavigation (60% of N/A stimulator)	**Fixation task:** VSTM orientation change detection task	Ipsi-/contra- & no TMS	250 ms	8	Percent correct
10	Saad et al. (2015)	Difference in VSTM and imagery neural bases	V1 (5p)	(1) Neuronavigation for n=N/A (2) Phosphene induction for n=N/A (90% of phosphene threshold for n=N/A or 65% of Magstim Rapid^2 stimulator for n=N/A)	Orientation change detection task	Sham TMS	2600 ms	15	Detection sensitivity
11	Koivisto et al. (2017)	TMS effects on quality of memory representations	Right and left V1 (sp)	Neuronavigation (65% of Nextim eXimia^{tm} stimulator)	VSTM orientation match task	**Exp1:** Ipsi-/ contra- & no TMS **Exp2:** Ipsi-/ contra- & no TMS	**Exp1:** -30 ms to 120 ms (30 ms intervals) **Exp2:** 120 ms, or 150 ms, or 180 ms	**Exp1:** 12 **Exp2:** 7	(1) Proportion of guessing (2) Precision
12	Rademark et al. (2017)	SVC role in VSTM	Right or left V1 (3p)	Neuronavigation (80% of phosphene threshold)	VSTM orientation match task	Ipsi-/contra- & Sham TMS	0 ms or 900 ms	8	(1) Absolute error (2) Precision (3) Guess frequency
13	van Lamsweerde et al. (2017)	SVC role in VSTM	Right V1 (sp)	Neuronavigation (110% of phosphene threshold)	**Exp3:** colour match to sample task	**Exp3:** ipsi-/ contra-	**Exp3:** 0 ms, 100 ms, or 200 ms	**Exp3:** 21	(1) Absolute error (2) Precision (3) Guess frequency (4) Swap errors

Tab 1. The included papers with short descriptions that were identified after following the PRISMA statement for a systematic approach in literature search.
Abbreviations: 3p; three pulses, 5p; five pulses, Exp; experiment, ROI; region of interest, sp; single pulse, TMS; transcranial magnetic stimulation, VSTM; visual short-term memory

Table 2: Experiments included in the meta-analysis of TMS on SVC during the encoding phase of a VSTM task.

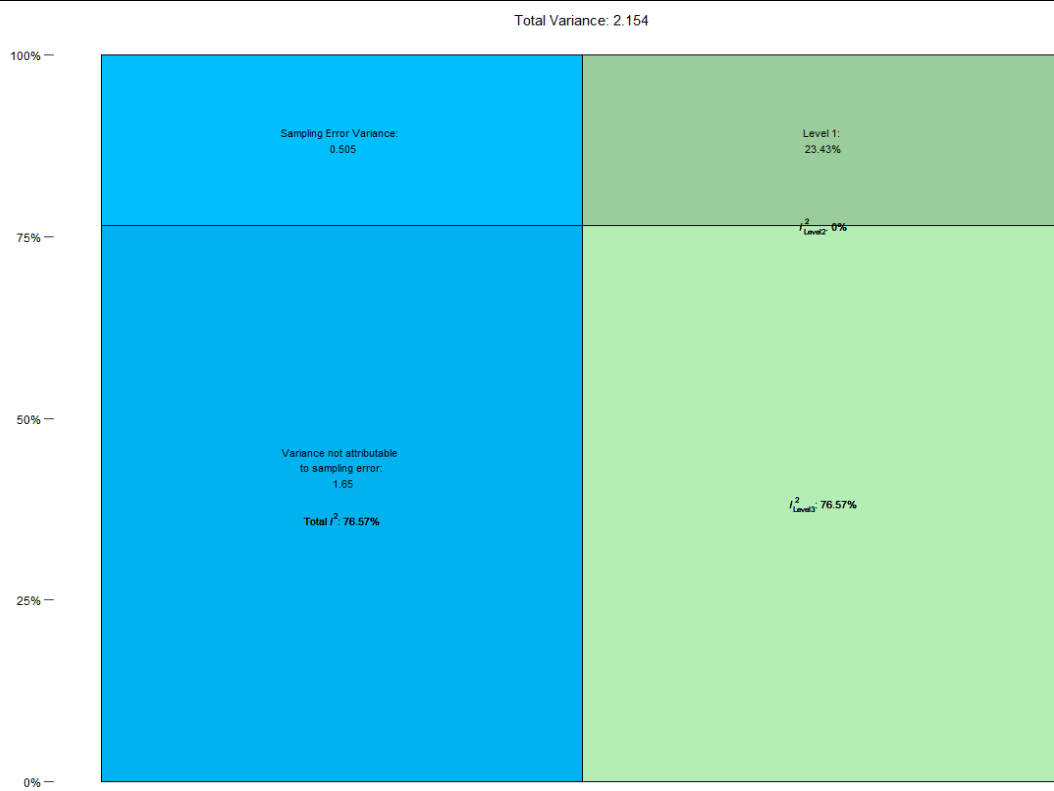|	STUDY	EFFECT SIZE	STANDARD ERROR	Z-VALUE	P-VALUE	N	BEHAVIOURAL MEASURE (condition)	CONTROL CONDITION
1	Cattaneo et al (2009)a	1.48	0.61	2.42	0.02	14	Accuracy	No TMS
2	Cattaneo et al (2009)b	1.15	0.58	1.97	0.05	14	Accuracy	Sham TMS
3	van de Ven et al (2012)a	-0.36	0.40	-0.91	0.36	13	Detection Sensitivity A' (LL)	Ipsilateral SVC
4	van de Ven et al (2012)b	-0.23	0.39	-0.59	0.56	13	Detection Sensitivity A' (HL)	Ipsilateral SVC
5	van de Ven et al (2012)c	0.00	0.39	0.00	1.00	13	Detection Sensitivity A' (LL)	Ipsilateral SVC
6	van de Ven et al (2012)d	-0.97	0.42	-2.33	0.02	13	Detection Sensitivity A' (HL)	Ipsilateral SVC
7	Koivisto et al (2017)a	3.45	0.66	5.25	0.00	12	Proportion of Guess (Exp1 60 ms)	No TMS
8	Koivisto et al (2017)b	3.81	0.70	5.44	0.00	12	Proportion of Guess (Exp1 90 ms)	No TMS
9	Koivisto et al (2017)c	3.15	0.62	5.05	0.00	12	Proportion of Guess (Exp1 120 ms)	No TMS
10	Koivisto et al (2017)d	0.42	0.54	0.78	0.44	7	Proportion of Guess (Exp2 120 ms)	Ipsilateral SVC
11	Koivisto et al (2017)e	0.64	0.55	1.17	0.24	7	Proportion of Guess (Exp2 150 ms)	Ipsilateral SVC
12	Koivisto et al (2017)f	0.09	0.53	0.17	0.86	7	Proportion of Guess (Exp3 150 ms)	Ipsilateral SVC
13	Koivisto et al (2017)g	0.22	0.54	0.40	0.69	7	Proportion of Guess (Exp2 120 ms)	No TMS
14	Koivisto et al (2017)h	0.50	0.54	0.91	0.36	7	Proportion of Guess (Exp2 150 ms)	No TMS
15	Koivisto et al (2017)i	0.06	0.53	0.11	0.91	7	Proportion of Guess (Exp3 150 ms)	No TMS
16	Rademark et al (2017)	0.32	0.50	0.63	0.53	8	Absolute Error	Sham TMS
17	van Lamsweerde et al (2017)a	1.05	0.47	2.24	0.03	21	Guess Rate (0 ms)	Ipsilateral SVC
18	van Lamsweerde et al (2017)b	0.20	0.44	0.46	0.65	21	Guess Rate (100 ms)	Ipsilateral SVC
19	van Lamsweerde et al (2017)c	0.41	0.44	0.94	0.35	21	Guess Rate (200ms)	Ipsilateral SVC

Tab 2. All effect sizes, standard errors, 95% confidence intervals, Z-values, p-values and weight calculated from the included studies that induced TMS during the encoding phase of a VSTM task. HL; high load condition, LL; low load condition, SVC; sensory visual cortex, TMS; transcranial magnetic stimulation, VSTM; visual short-term memory.

Figure 2: Meta-analysis of TMS on SVC during the encoding phase of a VSTM task.

A

Study	Effect Size	Standard Error	Standardised Mean Difference	g	95% CI	Wei
van de Ven et al (2012)d	-0.97	0.42		-0.97	[-1.79; -0.15]	5.
van de Ven et al (2012)a	-0.36	0.40		-0.36	[-1.14; 0.41]	5.
van de Ven et al (2012)b	-0.23	0.39		-0.23	[-1.00; 0.54]	5.
van de Ven et al (2012)c	0.00	0.39		0.00	[-0.77; 0.77]	5.
Koivisto et al (2017)i	0.06	0.53		0.06	[-0.99; 1.11]	5.
Koivisto et al (2017)f	0.09	0.53		0.09	[-0.96; 1.14]	5.
van Lamsweerde et al (2017)b	0.20	0.44		0.20	[-0.66; 1.06]	5.
Koivisto et al (2017)g	0.22	0.54		0.22	[-0.83; 1.27]	5.
Rademark et al (2017)	0.32	0.50		0.32	[-0.67; 1.30]	5.
van Lamsweerde et al (2017)c	0.41	0.44		0.41	[-0.45; 1.28]	5.
Koivisto et al (2017)d	0.42	0.54		0.42	[-0.64; 1.48]	5.
Koivisto et al (2017)h	0.50	0.54		0.50	[-0.57; 1.56]	5.
Koivisto et al (2017)e	0.64	0.55		0.64	[-0.44; 1.72]	5.
van Lamsweerde et al (2017)a	1.05	0.47		1.05	[0.13; 1.96]	5.
Cattaneo et al (2009)b	1.15	0.58		1.15	[0.01; 2.29]	5.
Cattaneo et al (2009)a	1.48	0.61		1.48	[0.28; 2.68]	4.
Koivisto et al (2017)c	3.15	0.62		3.15	[1.93; 4.37]	4.
Koivisto et al (2017)a	3.45	0.66		3.45	[2.16; 4.74]	4.
Koivisto et al (2017)b	3.81	0.70		3.81	[2.44; 5.18]	4.

Overall Effect   0.74 [0.20; 1.28] 100.

Heterogeneity: $I^2 = 80\%$ [70%; 87%], $\tau^2 = 1.1604$, $p < 0.01$

-4   -2   0   2   4
Control vs TMS

B

Fig 2. The meta-analysis of behavioural outcomes when inducing TMS on the SVC during the encoding phase of a VSTM task. (**A**) The forest plot of a random effects model pooling the effect sizes of experiments inducing TMS on SVC during the encoding phase of a VSTM task. The overall standard means difference indicates that TMS does have an effect on behaviour when induced on the SVC during the encoding phase of a VSTM task. (**B**) A funnel plot of the same experiments to investigate publication bias shows an asymmetry between the data points, indicating publication bias. SVC; sensory visual cortex, TMS; transcranial magnetic stimulation, VSTM; visual short-term memory.

Figure 3: The three-level meta-analysis model for VSTM encoding.

Fig 3. The distribution of variance in the three-model meta-analysis for VSTM encoding, where experiments were clustered to their corresponding studies to introduce the study level (level 2) in the meta-analysis. No variance was explained by level 2 in the three-level model. VSTM; visual short-term memory.

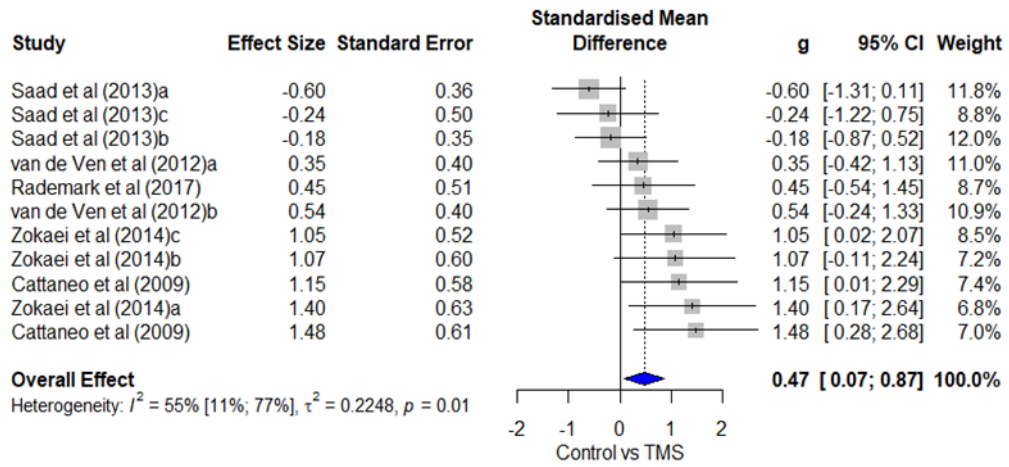**Table 3:** Experiments included in the meta-analysis of TMS on SVC during the maintenance phase of a VSTM task.

	STUDY	EFFECT SIZE	STANDARD ERROR	Z-VALUE	P-VALUE	N	BEHAVIOURAL MEASURE (condition)	CONTROL CONDITION
1	Cattaneo et al (2009)a	1.48	0.61	2.42	0.02	14	Accuracy	No TMS
2	Cattaneo et al (2009)b	1.15	0.58	1.97	0.05	14	Accuracy	Sham TMS
3	van de Ven et al (2012)a	0.35	0.40	0.89	0.38	13	Detection Sensitivity A' (LL)	Ipsilateral SVC
4	van de Ven et al (2012)b	0.54	0.40	1.36	0.17	13	Detection Sensitivity A' (HL)	Ipsilateral SVC
5	Saad et al (2013)a	-0.60	0.36	-1.67	0.09	16	Accuracy (Exp2 2000 ms)	Sham TMS
6	Saad et al (2013)b	-0.18	0.35	-0.49	0.62	16	Accuracy (Exp2 5000 ms)	Sham TMS
7	Saad et al (2013)c	-0.24	0.50	-0.47	0.64	8	Accuracy (Exp3 5000 ms)	Sham TMS
8	Zokaei et al (2014)a	1.40	0.63	2.23	0.03	13	Precision (Exp 1 congruent)	Sham TMS
9	Zokaei et al (2014)b	1.07	0.60	1.78	0.07	13	Precision (Exp 1 incongruent)	Sham TMS
10	Zokaei et al (2014)c	1.05	0.52	2.01	0.04	17	Precision (Exp 2 Item 1)	Sham TMS
11	Rademark et al (2017)	0.45	0.51	0.89	0.37	8	Absolute Error	Sham TMS

Tab 3. All effect sizes, standard errors, 95% confidence intervals, Z-values, p-values and weight calculated from the included studies that induced TMS during the maintenance phase of a VSTM task. HL; high load condition, LL; low load condition SVC; sensory visual cortex, TMS; transcranial magnetic stimulation, VSTM; visual short-term memory.
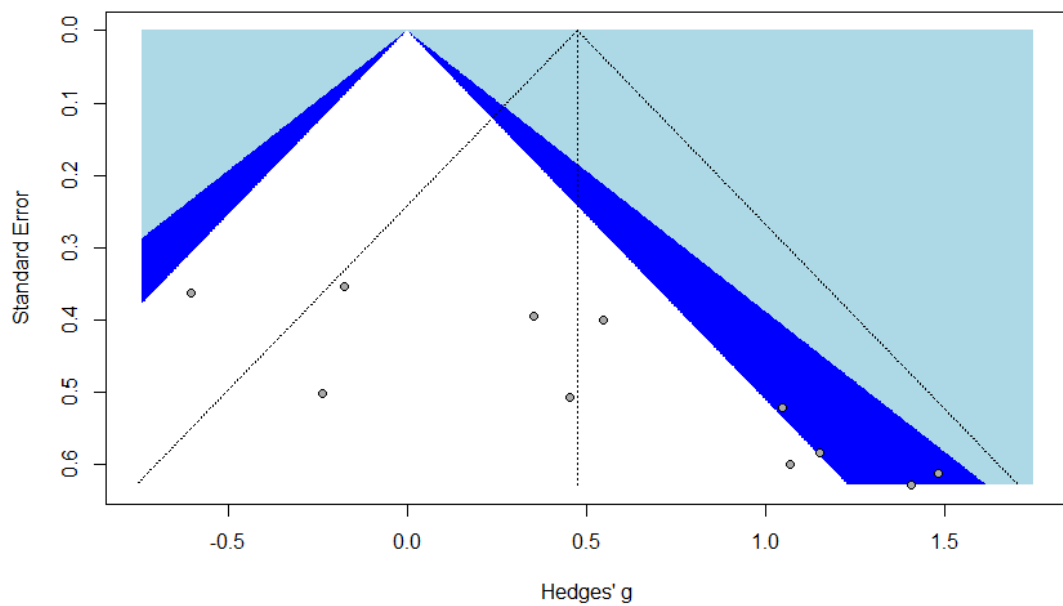
**Figure 4:** Meta-analysis of TMS on SVC during the maintenance phase of a VSTM task.

A

B

Fig 4. The meta-analysis of behavioural outcomes when inducing TMS on the SVC during the maintenance phase of a VSTM task. (**A**) The forest plot of a random effects model pooling the effect sizes of experiments inducing TMS on SVC during the maintenance phase of a VSTM task. The overall standard means difference indicates that TMS does have an effect on behaviour when induced on the SVC during the maintenance phase of a VSTM task. (**B**) A funnel plot of the same experiments to investigate publication bias shows an asymmetry between the data points, indicating publication bias. SVC; sensory visual cortex, TMS; transcranial magnetic stimulation, VSTM; visual short-term memory.

Figure 5: The three-level meta-analysis model for VSTM maintenance.
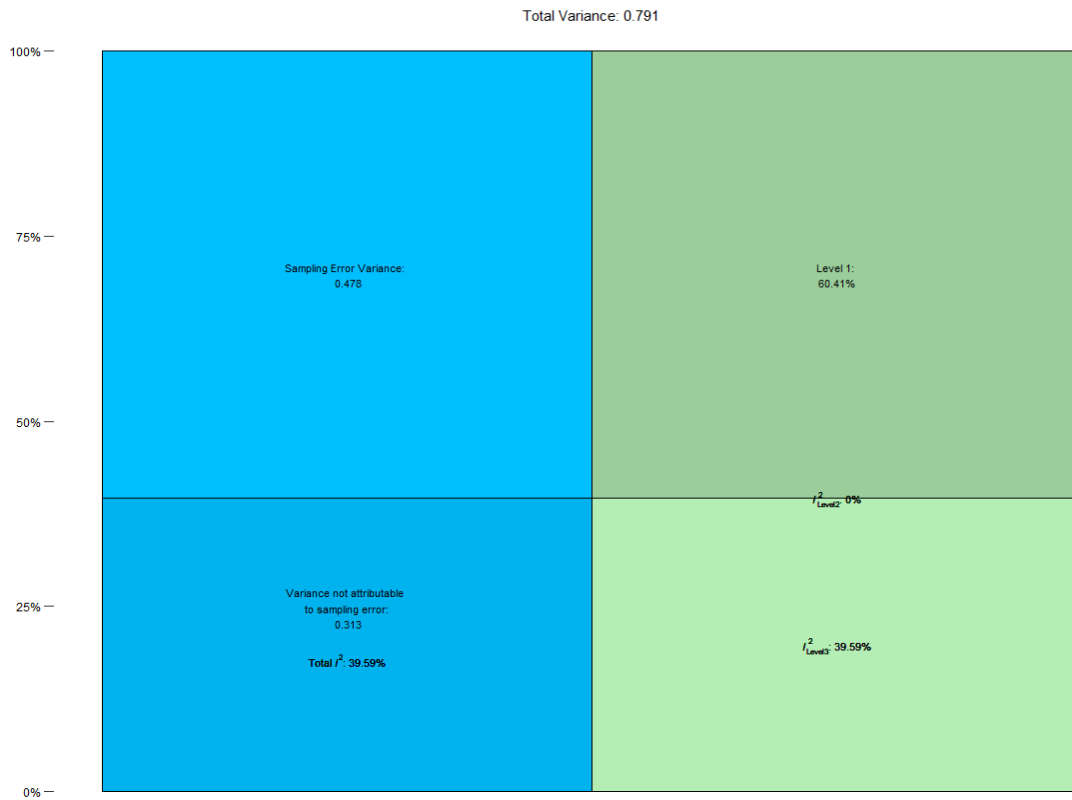
Fig 5. The distribution of variance in the three-model meta-analysis for VSTM maintenance, where experiments were clustered to their corresponding studies to introduce the study level (level 2) in the meta-analysis. No variance was explained by level 2 in the three-level model. VSTM; visual short-term memory.