Causal evidence for the role of the sensory visual cortex in visual short-term memory maintenance

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Abstract

The role of the sensory visual cortex during visual short-term memory (VSTM) remains controversial. This controversy is possibly due to methodological issues in previous attempts to investigate the effects of transcranial magnetic stimulation (TMS) on VSTM. This study aims to use TMS, while covering previous methodological deficits. Young adults will be recruited to participate in two experiments using a VSTM orientation change-detection under TMS. Monocular vision will be ensured using red-blue goggles combined with red-blue stimuli. Double-pulse TMS will be delivered at different times (Experiment 1: 0ms, 200ms, or 1000ms; Experiment 2: 200ms, 1000ms) during a 2 s retention phase, on one side of the occipital hemisphere (right hemisphere for 50% of the participants). In experiment 2, a sham-TMS condition will be introduced. Behavioural effects in the ipsilateral occipital hemisphere to visual hemifield will indicate a causal involvement of the sensory visual cortex during a specific temporal point in VSTM.

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

Visual short-term memory (VSTM) enables us to maintain in mind, for a short period of time, visual representations that are no longer present, in order to complete task-oriented goals. VSTM protects visual information against interference, making representations available for cognitive processing, and thus provides the essential link between perception and higher cognitive functions, underpinning our ability for complex thought and action (Luck & Vogel, 2013). For decades, cognitive scientists have studied the neural correlates of VSTM, establishing the role of specific brain areas such as the prefrontal and parietal areas in VSTM (Bettencourt & Xu, 2016; Christophel et al., 2017; Ester et al., 2015, Ester, Rademaker, et al., 2016; Funahashi, 2017; Lee et al., 2013; Mendoza-Halliday et al., 2014; Riley & Constantinidis, 2016; Smith & Jonides, 1999; Stokes, 2015; Xu, 2017, 2020, 2021). Although much research has attempted to understand the neural architecture of VSTM, it is still unclear if activity in the sensory visual cortex (area V1) is required for successfully maintaining visual information in short-term memory. Even though it is established that the sensory visual cortex is primarily engaged in encoding visual information (D'Esposito & Postle, 2015; de Graaf et al., 2014; Kamme, 2007; Serences, 2016, Xu, 2017), results are controversial when it comes to its involvement in VSTM maintenance (Awh & Jonides, 2001; Christophel et al., 2017; D'Esposito & Postle, 2015; Lorence Lorence & Sreenivasan, 2021; Serences, 2016; Sreenivasan et al., 2014; Tapia & Beck, 2014; Teng & Postle, 2021; van de Ven & Sack, 2013; Xu, 2017, 2020, 2021).

Traditionally, VSTM was investigated under the scope of sustained neural activity (Leavitt et al., 2017), suggesting that during VSTM tasks, neural activity potentials are maintained online in frontal and parietal cortical areas (e.g., Chafee & Goldman-Rakic, 1998; Funahashi et al., 1989). However, more recently this traditional view has been challenged (Lundqvist et al., 2018; Masse et al., 2020; Stokes, 2015) following methodological advances in computational methods of neuroimaging data. Specifically, using multivariate analyses, it has been shown that VSTM contents can be decoded in the sensory visual area, in the absence of sustained brain activity (Harrison & Tong, 2009; Serences et al., 2009). In addition, early visual brain areas were shown to respond to specific visual features during VSTM maintenace, such as orientation (Harrison & Tong, 2009; Issa et

al., 2008; Serences et al., 2009), contrast (Konstantinou et al., 2012), and direction of movement (Bisley & Pasternak, 2000). These findings led to the introduction of the sensory recruitment hypothesis, according to which sensory visual cortex is an essential part of the brain network responsible for successfully maintaining information about elemental visual features in VSTM (Serences, 2016; Harrison & Tong, 2009; Pasternak & Greenlee, 2005; Postle, 2005; Serences et al., 2009; Supèr et al., 2001; for recent reviews see Lorence & Sreenivasan, 2021; Teng & Postle, 2021). In summary, this evidence indicated that early visual areas (such as area V1) have a dual function: they are responsible for the precise sensory encoding of elemental visual features (e.g., contrast, orientation, spatial frequency, direction of motion, speed of motion), and the short-term maintenance of this information.

Indeed, sensory visual cortex neurons are ideal candidates for short-term maintenance because they exhibit highly selective tuning for specific visual features. Utilizing specialized regions of the visual cortex to support VSTM might be a highly efficient way to avoid recoding remembered information in other distal networks. Moreover, the high degree of the sensory visual cortex selectivity is not observed in higher-order areas, whereas such selectivity is critical for remembering subtle distinctions between stimuli. Even though evidence using multivariate analyses has supported stimulus-specific activation in frontal and parietal areas (Christophel et al., 2018; Ester, Sutterer, et al, 2016), this view has recently been contended (Postle & Yu, 2020). However, others have argued that storing information in sensory visual cortex leaves memory representations susceptible to overwriting as new stimuli are processed, and that networks in sensory areas are not sufficiently wired to support the type of recurrent activity thought to support VSTM (Xu, 2017, 2020, 2021). Given that higher-order brain areas lack the visual selectivity of early sensory areas, it is still unclear how people can maintain specific visual features, such as the precise orientation of a visual stimulus, with minimal decay over some seconds (Magnussen & Greenlee, 1999).

The controversial evidence regarding sensory recruitment (Awh & Jonides, 2001; Christophel et al., 2017; D'Esposito & Postle, 2015; Lorence & Sreenivasan, 2021; Serences, 2016; Sreenivasan et al., 2014; Tapia & Beck, 2014; Teng & Postle, 2021; Xu, 2017, 2020, 2021) has driven a debate in the current literature as to whether the sensory visual cortex is indeed involved in VSTM maintenance (Gayet et al., 2018; Scimeca et al., 2018) or whether its role is restricted to the perception of visual information (Xu, 2017, 2018, 2020, 2021). Researchers have implemented many methodological approaches, such as functional magnetic resonance imaging (fMRI) and psychophysical experiments, but have yielded mixed results (e.g., Bettencourt & Xu, 2016; Harrison & Bays, 2018; Rademaker et al., 2019; Yörük et al., 2020). Several reasons have been proposed to explain these mixed results, such as activity silent mechanisms, feed-forward processes, lack of causal evidence, methodological differences and in some cases methodological oversights (D'Esposito et al., 1999; D'Esposito & Postle, 2015; Lorence & Sreenivasan, 2021; Masse et al., 2020; Serences, 2016; Teng & Postle, 2021; Xu, 2017, 2020, 2021). An ideal hypothetical scenario for investigating whether sensory visual cortex is required for VSTM maintenance would involve its complete inactivation during the retention interval of a VSTM task and reactivation at the onset of the memory probe display (Gayet et al., 2018). Such an experimental design could yield causal evidence as to whether the sensory visual cortex is a necessary component of the brain network responsible for the short-term maintenance of elemental visual features. Although such an experiment is impossible to be carried out, brain stimulation using transcranial magnetic stimulation (TMS) during the retention interval of a VSTM task can approximate this scenario. TMS uses a coil to transfer electromagnetic stimulation at localized brain areas. TMS targeted at the sensory visual cortex has been shown to directly interfere with cortical activity, making the exploration of causal evidence plausible (de Graaf et al., 2014; Pitcher et al., 2020; Tapia & Beck, 2014).

Previous studies have attempted to investigate the role of the sensory visual cortex in VSTM using TMS, combined with delayed change detection or match-to-sample tasks (Cattanea et al., 2009; Jia et al., 2021; Rademaker et al., 2017; Silvanto & Cattaneo, 2010; van de Ven & Sack, 2012;

van Lamsweerde & Johnson, 2017). In these tasks, a memory array (i.e. set of stimuli that participants are asked to remember) is presented to participants, followed by a maintenance delay period. Subsequently, participants are requested to compare (or match) a probe with the earlier memory array. The sensory visual cortex is stimulated at different points during the maintenance delay period, in order to make causal inferences based on the temporal point of the TMS interference. In most experiments, stimulation was induced on the sensory visual cortex of one hemisphere, while stimuli were presented either in the ipsilateral or contralateral (to the stimulation site) visual hemifield in a counterbalanced manner (Cattaneo et al., 2009; Rademaker et al., 2017; van de Ven & Sack, 2012; van Lamsweerde & Johnson, 2017). To draw evidence and reach a conclusion, comparisons between the ipsilateral versus the contralateral conditions (Cattaneo et al., 2009; Rademaker et al., 2017; van de Ven & Sack, 2012; van Lamsweerde & Johnson, 2017), and between real versus sham TMS (Cattaneo et al., 2009; Jia et al., 2021; Rademaker et al., 2017; Silvanto & Cattaneo, 2010) were considered.

As with different methodological approaches, results from previous TMS studies were mixed with regards to the sensory recruitment hypothesis. Specifically, some of the studies supported the sensory recruitment hypothesis (Cattaneo et al., 2009; Jia et al., 2021; Silvanto & Cattaneo, 2010), some rejected it (Rademaker et al., 2017; van Lamsweerde & Johnson, 2017), while others were unclear (van de Ven et al., 2012). After a careful examination of the methods used in previous TMS studies, we suggest that the inconclusive findings are due to several important methodological issues that may have underestimated the contribution of the sensory visual cortex in VSTM. The most vital issue in the majority of these TMS studies is that previous researchers considered that, when information was presented on one side of the visual hemifield (either right or left side near the centre of the monitor), the contralateral sensory visual cortex processed it. Therefore, stimuli were always presented binocularly to the participants either in the left or right visual field, and a contralateral sensory visual cortex TMS was applied to be compared to an ipsilateral control condition (see Figure 1A). However, considering the neuroanatomy of the visual pathway system,

the binocular presentation of stimuli either left or right close to the midline of the visual field -as was the case in the majority of the previous studies- does not accurately correspond to the contralateral sensory visual cortex, and could in fact be processed by the ipsilateral one if presented withing 15^{o} of visual angle from midline (Joukal, 2017; Wichmann & Müller-Forell, 2004). Also, given the neural bases of the visual system, it is possible that information enters the sensory visual cortex in both brain's hemispheres (Tong et al., 2006) since the visual field of both eyes overlaps in certain areas (within 15° of visual angle) of the visual field (see Figure 1B; Wichmann & Müller-Forell, 2004). Consequently, some TMS effects can be falsely interpreted or remain undetectable (e.g., if information processing happens in both hemispheres despite the contralateral and ipsilateral conditions; de Graaf & Sack, 2011; see also Pitcher et al., 2020).

Another important shortcoming relates to the stimuli used in the memory array. Previous TMS studies used various stimuli in their memory tasks, some of which included complex stimuli such as abstract shapes (van de Ven et al., 2012). However, the evidence leading to the sensory recruitment hypothesis emphasized the selective engagement of the sensory visual cortex in elemental visual features (Harrison & Tong, 2009; Issa et al., 2008; Konstantinou et al., 2012; Serences et al., 2009). Furthermore, a parallel literature, has shown that increased object complexity can increase information load, thereby limiting VSTM capacity (Alvarez & Cavanagh, 2004). Hence, it is possible that some of the previous studies failed to find evidence of the sensory visual cortex's involvement in VSTM due to using complex stimuli (i.e., exceeding V1 capacity).

Therefore, in order to provide causal evidence for the role of the sensory visual cortex during VSTM more reliably, the methodological limitations of previous TMS studies need to be addressed. In particular, the two visual hemifields must be reliably separated so that the visual input is processed by only one occipital hemisphere. One way to reliably separate the sensory visual cortex hemisphere that processes the information entering the visual field, is to present the stimuli monocularly. To achieve monocular stimulus presentation, similar methodological principles as

those used in binocular rivalry can be implemented (Carmel et al., 2010). In binocular rivalry, different images overlapping in the visual field are presented separately to each eye. Therefore, by presenting an image corresponding only to one eye (thus avoiding rivalry), stimuli will enter the sensory visual cortex monocularly (Polonsky et al., 2010). Also, given the V1 neuronal response to specific visual features, the memory array should consist of an elemental visual feature known to selectively correspond to the sensory visual cortex, such as orientation (Harrison & Tong, 2009; Issa et al., 2008; Jia et al., 2021; Serences et al., 2009; Swisher et al., 2010).

In short, the objective of the current study is to provide causal evidence for the role of the sensory visual cortex during VSTM maintenance using TMS, while ensuring monocular vision. In the proposed experiments, stimuli will be presented in the center of the visual field to be viewed monocularly. Therefore, based on the neuroanatomy of the visual pathway (Joukal, 2017; Tong et al., 2006; Wichmann & Müller-Forell, 2004), it is expected that visual information will initially be processed solely by the ipsilateral (to the eye receiving the information) sensory visual cortex. As a result, and contrary to past experiments, the contralateral sensory visual cortex will be the control condition. We propose to test the hypothesis that, when visual stimuli are presented monocularly, participants' average detection sensitivity (Stanislaw & Todorov, 1999), accuracy, and response time in a delayed change-detection VSTM task will not differ between the ipsilateral and contralateral conditions when TMS is applied (1) during perceptual processing (baseline condition; 0 ms after stimulus onset), (2) during early information maintenance (200 ms after stimulus onset), or (3) during late information maintenance (1000 ms after stimulus onset). Moreover, in a second experiment, we will test whether VSTM performance differs between a TMS and a sham TMS condition (1) during encoding (200 ms after stimulus onset) and (2) during memory maintenance (1000 ms after stimulus onset). Table 1 presents the research hypotheses for each experiment.

Methods

Ethics information

The study has been approved by the Cyprus National Bioethics Committee (ΕΕΒΚ/ΕΠ/2016/37).

Design

Apparatus and stimuli

A Magstim Super Rapid^2 (MagStim, Whitland, Wales, UK SA34 OHR) stimulator will be used for inducing TMS. A D70 Alpha Flat Coil (Uncoated) will deliver a double-pulse TMS at the different experimental conditions, while an identical sham coil will be used to control for noise and other TMS artefacts (in Experiment 2). The double-pulse TMS will be induced with a frequency of 10Hz, meaning that stimulation will be delivered by two pulses separated by a duration of 100 ms. The stimuli and all experimental procedures will be designed and controlled using Python and PsychoPy (Peirce et al., 2019), which will be run on an HP PRODESK desktop computer. To control the TMS, the MagPy TMS package will be used (McNair, 2017). Stimuli will be presented on a 21.5" Philips 226V^{la} monitor with a 60Hz refresh rate. A chinrest will be placed to ensure that participants maintain a viewing distance of 57 cm from the monitor. Stimuli will consist of either a red or a blue grating (i.e., Gabor patch) which will be oriented either horizontally or with a clockwise or counter-clockwise tilt from the horizontal axis, presented on a black background (Figure 2). The diameter of the grating will be 1° (in degrees of visual angle). Stimuli will be presented at fixation. To ensure that stimulus will be viewed monocularly, stimuli will be viewed through red/blue anaglyph goggles, consistent with previous research (Haynes et al., 2005), where red stimuli will only be viewed by the left eye and blue stimuli only by the right eye (Carmel et al., 2010).

Experimental design

Two experiments using the same delayed change-detection task will be carried out. Participants will be asked to compare the orientation of a probe to the orientation of a remembered

grating (memory array) after a 2 second delay period (Figure 2). In half the trials, the probe will have the same orientation as the memory array. In the other half, the probe will be oriented clockwise (25% of the trials) or counter-clockwise (25% of the trials) to the remembered grating (Figure 2).

Experiment 1 is designed to allow for within-subject comparisons between the ipsilateral and contralateral stimulation conditions at three different TMS timing conditions. Timing conditions refer to the temporal distance of the stimulation after the memory grating's onset. The 0 ms timing condition, will work as a baseline control measurement. Specifically, the first TMS pulse is induced at the onset of the stimulus and the second TMS pulse when the stimulus presentation finishes (at 100 ms). Thus, given the established role of the sensory visual cortex during visual perception (D'Esposito & Postle, 2015; de Graaf et al., 2014; Kamme, 2007; Serences, 2016, Xu, 2017), a significant drop in VSTM performance (decreased detection sensitivity and accuracy) is expected in the ipsilateral compared to the contralateral condition. The 200 ms condition (first TMS pulse at 200 ms after stimulus onset and second TMS pulse 300 ms after stimulus onset) will shed light on the role of the sensory visual cortex during the early maintenance phase of VSTM, while the 1000 ms condition (first TMS pulse at 1000 ms after stimulus onset and second TMS pulse 1100 ms after stimulus onset) will allow the exploration of its role during the later maintenance period. These conditions lead to a two (ipsilateral/contralateral) by three (0ms/200ms/1000ms) design. A total of 360 trials (120 trials per timing condition; 60 with ipsilateral TMS and 60 with contrallateral TMS in each timing condition) will be gathered, which will be divided into six blocks of 60 trials and presented in a counterbalanced manner across participants.

Experiment 2 aims to replicate the effects that will be obtained in Experiment 1, while controlling for other factors that may cause or hinder our experimental effects, by adding a sham-TMS control condition. In addition to controlling for TMS noise and other artefacts, a sham TMS control is important for three reasons. First, TMS interference may affect both hemispheres due to the visual input being processed by both hemispheres and thus any actual effects remain undetected

(de Graaf & Sack, 2011; Pitcher et al., 2020). Since Experiment 1 compares an ipsilateral with a contralateral condition, where stimulation is always present, it is plausible that TMS noise interferes in such a way, that an effect in behaviour is always present. Thus, if the additional noise by TMS affects the baseline condition, then comparisons between the ipsilateral and contralateral stimulation condition might not indicate any significant difference. By introducing a sham TMS condition, Experiment 2 will control for this possibility, allowing comparisons between real and sham stimulation. Second, it is likely that the sensory visual cortex processes information in both hemispheres (e.g., due to feedforward and feedback mechanisms; King & Wyart, 2019) so that stimulating only one of the two hemispheres is not enough to affect behavioural measures. Lastly, contrary to previous research, we suggest that visual information will be initially processed by the ipsilateral sensory visual cortex when the stimulus is presented within approximately 15^{o} of visual angle from midline (Joukal, 2017; Tong et al., 2006; Wichmann & Müller-Forell, 2004). However, without a sham control condition, it would be impossible to correctly interpret the direction of any possible effect. Specifically, in previous experiments, TMS was shown to either facilitate (Cattaneo et al., 2009) or hinder (Jia et al., 2021; van de Ven et al., 2012) performance. It should be pointed out, that the interpretations of such effects are unavoidably biased by the hypotheses. For example, if an effect is expected in the contralateral site, an increased performance might be interpreted as a facilitation effect but might, in reality, be due to hindering effects in the ipsilateral condition. Thus, given the neural basis of the visual pathway (Joukal, 2017; Tong et al., 2006; Wichmann & Müller-Forell, 2004), along with the possible feedforward and feedback mechanisms of the sensory visual cortex (e.g., Miller et al., 1996; Van Kerkoerle et al., 2017; see also King & Wyart, 2019), this is an important factor that must be controlled for. Therefore, Experiment 2, will allow comparisons between actual and sham stimulation on behaviour. Since sham TMS is introduced in Experiment 2, which will work as a baseline measurement, the 0 ms condition that worked as a baseline in Experiment 1 will be dropped. Therefore, in Experiment 2, only two timing conditions will be used, at 200 ms (first TMS pulse at 200 ms after stimulus onset and second TMS pulse 300 ms after stimulus

onset) and 1000 ms (first TMS pulse at 1000 ms after stimulus onset and second TMS pulse 1100 ms after stimulus onset), corresponding to an early maintenance phase and a late maintenance phase of VSTM respectively. As in Experiment 1, the timing conditions refer to the temporal distance between stimulation and memory array onset. This leads to a within-subject design, comparing differences between the ipsilateral and contralateral conditions, at two different TMS timing conditions, and two different stimulation conditions. These conditions create a two (ipsilateral/contralateral) by two (200 ms/1000 ms) by two (TMS/sham TMS) design. In total, 512 trials (256 TMS conditions; 128 per timining condition out of which 64 ipsilatteraly and 64 contrallateraly and 256 sham TMS conditions; 128 per timing condition 64 ipsilatteraly and 64 contrallateraly) will be collected, which will be divided into eight blocks of 64 trials and presented across participants in a counterbalanced fashion.

Procedure

Sensory visual cortex stimulation. Before the main experiment, we will localise the right or left sensory visual cortex of each participant (Cattaneo et al., 2009; Silvanto & Cattaneo, 2010; van de Ven et al, 2012) using the functional method of eliciting phosphenes (Walsh & Pascual-Leone, 2003) and the localization will be counterbalanced across participants. Specifically, a tight cap will be placed on each participant's head and the inion will be marked. Participants will be blindfolded but instructed to keep their eyes open using a hollow blindfold. The coil will be placed two centimetres above the inion and one centimetre laterally (either left or right based on the participant's group). Starting at a 60% TMS output power, a double-pulse TMS will be delivered and participants will orally report whether they have seen phosphenes or not (by saying outloud "yes" or "no"). If no phosphenes are reported after three consecutive stimulations, the procedure will be repeated by moving the coil in a one-by-one centimetre grid around the initial stimulation point by approximately 0.2 centimetres, inducing three single-pulse TMS at each position. If a participant still fails to report phosphenes, the same procedure will be repeated with a 5% increase on the stimulator output until phosphenes are reported, or until an 80% power on the stimulator has been reached. If participants fail to report phosphenes, the localization procedure will be repeated on the

opposite cortex and if they still fail to perceive phosphenes, a fixed output set at 65% of the stimulator's maximum output will be used, as has been done previously (Cattaneo et al., 2009; Koivisto et al., 2017; Saad et al., 2015). When the participants successfully report phosphenes, a mark will be placed on the cap and a mechanical arm will stabilize the TMS coil and together with the chinrest, this will hold the participant's head stable on that point. Three additional single pulses will be induced to confirm that participants experience phosphenes, and thus the coil is placed correctly.

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

To account for individual differences and avoid ceiling or floor effects in task performance, additional procedures will be conducted before the main experiments. Specifically, the task will be adjusted to each participant's perceptual ability to discriminate between orientation changes. A custom staircase procedure will be implemented, where participants will have to report whether a grating has a clockwise or counterclockwise tilt from the horizontal axis. According to each

participant's responses, the degrees of this tilt will either decrease (when three consecutive correct responses are given) or increase (when a response is incorrect). An approximation of accurately discriminating the orientation difference 75% of the time will be obtained by calculating the mean of the intervals where degree differences change direction (i.e., from an increase in degrees to a decrease and vice versa). The gratings used in this staircase will be identical to the experimental stimuli and so this procedure will be done twice, separately for the blue and red stimuli. For the main experiment, the orientation thresholds both for the red and blue stimuli will be increased by 20%, to account for the increased cognitive demands of the main task. Furthermore, before the two main experiments, participants will carry out a practice block of 24 trials without TMS stimulation to familiarise themselves with the experimental procedure.

Experiment 1. Each trial will begin with a screen indicating the trial number for each block. To proceed to the next trial, participants will need to press the 'spacebar' key on the keyboard. Next, a 500 ms white fixation dot will appear on the centre of a black background, followed by the memory grating for 100 ms. The stimulus grating will either have a horizontal orientation (50% of trials), a clockwise (25% of trials) or counter-clockwise (25% of trials) tilt. The tilt angle will be fixed across all trials for each participant at the level determined using the staircase procedure described above. From stimulus onset, a 2000 ms delay period indicated by a centred fixation dot will follow. Double-pulse TMS will be pseudorandomly delivered at one of three different timing conditions after the memory onset; either 0 ms, 200 ms, or 1000 ms. At the end of the retention period, a probe stimulus will appear. In half trials, the probe will be the same as the memory array stimulus. In the remaining 50% trials, the probe will be different as follows: if the memory array was horizontal, the probe will be tilted clockwise (25% of the different-condition trials) or counter-clockwise (25% of the different-condition trials). If the memory array stimulus was tilted, then the probe will be horizontal (50% of the different-condition trials). Participants will respond by placing their index and middle fingers on the arrow keys on the keyboard, indicating whether the orientation of the probe is the

same (index finger; 'left arrow key') or different (middle finger; 'down arrow key') compared to the memory array grating.

Experiment 2. The second experiment will use the same delayed change-detection VSTM task as in Experiment 1. The difference in Experiment 2 is the introduction of a sham coil that will deliver sham stimulation. TMS and sham TMS conditions will be blocked in a counterbalanced order. In addition, given the sham TMS condition, the baseline (0 ms TMS timing) will be dropped.

Sampling plan

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

For Experiment 1, sample updating with a stopping rule has been set to $BF_{10} > 3$ or $< 1/3$ for the Bayesian repeated measures ANOVA. However, due to counterbalancing, a minimum of 20 participants will be gathered (to ensure counterbalancing) or a maximum of 30 participants, given time and resource constraints. The same sample updating process with a stopping rule ($BF_{10} > 3$ or $< 1/3$) is set for Experiment 2 for the Bayesian repeated measures ANOVA. Similarly, a minimum of 20 participants will be gathered (to ensure counterbalancing) or a maximum of 30 participants (due to constraints). Therefore, the total number of participants for both experiments will range between 40 to 60 people.

Analysis plan

Analyses will be conducted using Jamovi (The Jamovi Project, 2021), an openly available R-based statistical software.

Experiment 1. The independent variables in Experiment 1 will be the three TMS timing conditions and comparisons will be made between the ipsilateral and contralateral conditions. Since monocular vision will be ensured, the ipsilateral condition refers to the situation where the TMS localised site (for example, right sensory visual cortex) is on the same side as the eye processing the stimulus (for example, right eye, and consequently the blue stimulus). The contralateral condition corresponds to when the TMS localised site (for example, right sensory visual cortex) does not match the side of the eye processing the stimuli (for example, left eye, and consequently red stimulus).

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

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

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

A 2 x 3 Bayesian repeated measures ANOVA will be implemented, where TMS site (ipsilateral/contralateral) by TMS timing (0ms, 200ms, 1000ms) will test the effects on *d'*. The Bayesian repeated measures ANOVA will indicate which model or interaction better represents the data. Further, we will perform Baysian paired t-tests between the TMS site difference for each TMS timing condition, in order to calculate a Bayes Factor. The Bayes Factor will indicate the likelihood ratio of each alternative hypothesis over the null hypothesis (BF_{10}), thus providing evidence for the likelihood of both hypotheses.

The repeated measures ANOVA will be performed using a random model with an r-scale = .83, according to recent meta-analytic findings (Phylactou et al., 2021). Each prior for the paired t-

tests is described by a Cauchy distribution centered around zero (see Rouder et al., 2009). The width parameter of each prior was calculated to correspond to the 90% probability of the effect size lying within the standardised differences (Hedge's g) reported in a recent meta-analysis on the topic (Phylactou et al., 2021). By considering the overall effect size (g = .83), the effect size for early TMS (up to 200 ms; g = .99), and the effect size for late TMS (after 200 ms; g = .65) from previous meta-analytic work (Phylactou et al., 2021), the width parameter of the Cauchy distribution was calculated to correspond to 0.132 for the 0 ms condition, to 0.156 for the 200 ms condition, and to 0.102 for the 1000 ms condition, respectively.

Experiment 2. In Experiment 2, the independent variables will be the two TMS timing conditions and comparisons will be made between the real and sham TMS conditions, as well as the ipsilateral and contralateral conditions.

As in Experiment 1, the dependent variable that will be examined is *d'*. A 2 x 2 x 2 Bayesian repeated measures ANOVA using a random model (r = .83) will be calculated, corresponding to the TMS site (ipsilateral/contralateral) by TMS (real/sham) by TMS timing (200ms, 1000ms). The priors which will be used for the paired t-tests are described as a Cauchy distribution with a width set to 0.156 for the 200 ms condition and 0.102 for the 1000 ms condition.

Data and code availability

The authors are committed to sharing all data, code and materials used in this study upon Stage 2 acceptance.

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Author contributions

PP and NK contributed equally to the conceptualization of the study. The final experimental design was completed with the support of AS. Equal contributions are expected for the experimental paradigm programming, data collection, and data analysis. PP prepared the original draft while NK and AS reviewed and edited the manuscript. NK acquired funding for the project.

Competing interests

The authors declare no competing interests.

Tables and Figures

Table 1: Design Table

Question	Hypothesis	Sampling plan	Analysis Plan	Interpretation given to different outcomes
Experiment 1				
Does double-pulse TMS on one hemisphere's sensory visual cortex during a VSTM with binocular rivalry affect detection sensitivity (*d'*) differently between the contralateral and ipsilateral conditions?	$H1_0$: Within participants, mean *d'* will not differ between the ipsilateral and contralateral condition when TMS is applied 0 ms after stimulus onset.	Sample updating with a stopping rule set at BF > 3 or BF < 1/3. Healthy individuals with normal or corrected to normal color vision. To ensure counterbalancing a minimum of 20 participants will be recruited. Due to time and resource constraints a maximum of 30 participants will be recruited.	2 (site; contralateral vs ipsilateral) x 3 (time; 0 ms, 200 ms, 1000 ms) repeated measures ANOVA. Bayesian paired t-test for post-hoc analyses. The prior is didscribed by a Cauchy prior centered around zero. Cauchy distribution width for each condition: 0 ms = .132 200 ms = .156 1000 ms = .102	The BF will indicate the likelihood of the alternative hypothesis (i.e., the difference in *d'* between ipsilateral and contralateral TMS does not equal to 0) over the null hypothesis. Evidence in favor of the alternative hypothesis for a distribution centered < 0 indicates a suppression TMS effect. Contrary, evidence for a distribution > 0 indicates a facilitation TMS effect. Evidence in support of the alternative hypothesis supports the causal involvement of the sensory visual cortex during visual perception. Evidence in support of the null hypothesis indicates that the sensory visual cortex is not involved during

				visual perception.
	$H2_0$: Within participants, mean *d'* will not differ between the ipsilateral and contralateral condition when TMS is applied 200 ms after stimulus onset.			Evidence in favor of the alternative hypothesis for a distribution centered < 0 indicates a suppression TMS effect. Contrary, evidence for a distribution > 0 indicates a facilitation TMS effect. Evidence in support of the alternative hypothesis supports the causal involvement of the sensory visual cortex during early information maintenance. Evidence in support of the null hypothesis indicates that the sensory visual cortex is not involved during early information maintenance.
	$H3_0$: Within participants' average *d'* will not differ between the ipsilateral and contralateral condition when TMS is applied 1000 ms after stimulus onset.			Evidence in favor of the alternative hypothesis for a distribution centered < 0 indicates a suppression TMS effect. Contrary, evidence for a distribution > 0 indicates a facilitation TMS effect. Evidence in support of the

				alternative hypothesis supports the causal involvement of the sensory visual cortex during late information maintenance. Evidence in support of the null hypothesis indicates that the sensory visual cortex is not involved during late information maintenance.
Experiment 2				
Does double-pulse TMS on one hemisphere's sensory visual cortex during a VSTM with binocular rivalry affect detection sensitivity (*d'*) differently compared to sham TMS?	$H4_0$: Within participants, mean *d'* will not differ between the TMS and sham TMS condition when TMS is applied 200 ms after stimulus onset.	Power analysis: N=21 (δ=.85, α=.05, β=.95) Given the counterbalanced design, 26 participants will be recruited. Individuals with normal or corrected to normal colour vision.	2 (site; contralateral vs ipsilateral) x 2 (time; 200 ms, 1000 ms) x 2 (TMS; real, sham) repeated measures ANOVA. Bayesian paired t-test for post-hoc analyses. The prior is didscribed by a Cauchy prior centered around zero. Cauchy distribution width for each condition: 0 ms = .132 200 ms = .156 1000 ms = .102	The BF will indicate the likelihood of the alternative hypothesis (i.e., the difference in *d'* between ipsilateral real TMS and ipsilateral sham TMS does not equal to 0) over the null hypothesis. Evidence in favor of the alternative hypothesis for a distribution centered < 0 indicates a suppression TMS effect. Contrary, evidence for a distribution > 0 indicates a facilitation TMS effect. Evidence in support of the alternative hypothesis supports the causal involvement of the sensory

				visual cortex during early information maintenance. Evidence in support of the null hypothesis indicates that the sensory visual cortex is not involved during early information maintenance.
	$H5_0$: Within participants, mean *d'* will not differ between the TMS and sham TMS condition when TMS is applied 1000 ms after stimulus onset.			Evidence in favor of the alternative hypothesis for a distribution centered < 0 indicates a suppression TMS effect. Contrary, evidence for a distribution > 0 indicates a facilitation TMS effect. Evidence in support of the alternative hypothesis supports the causal involvement of the sensory visual cortex during late information maintenance. Evidence in support of the null hypothesis indicates that the sensory visual cortex is not involved during late information maintenance.

Figure 1: Stimuli and experimental procedure

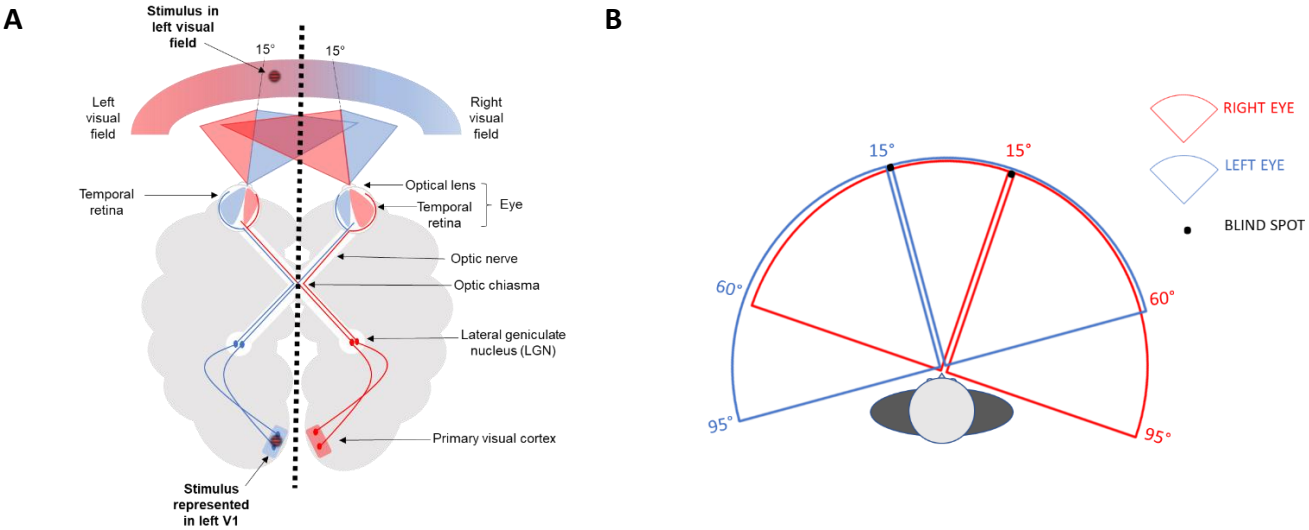

Fig.1 (A) In dichoptic presentation (represented by black vertical dotted line), a stimulus presented on the left visual field cannot be perceived by the right eye and it is therefore represented only in the ipsilateral V1 (i.e., left V1 in this example). (B) Visual field angle of the left and right eye. Stimuli presented within 15° of visual angle off of fixation are perceived by both eyes.

Figure 2: Stimuli and experimental procedure

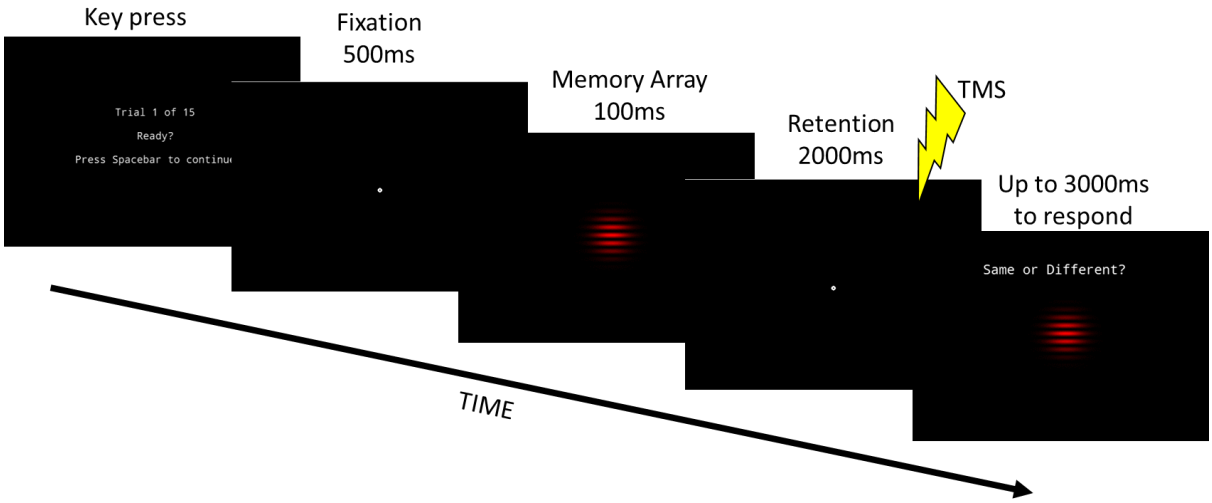

Fig.2 An example of the delayed change-detection task used in Experiments 1 and 2. The trial begins with a screen indicating the trial number, requesting a keypress to proceed. This is followed by a 500 ms fixation dot. Next, the memory array, consisting of either a red or blue Gabor patch, is shown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