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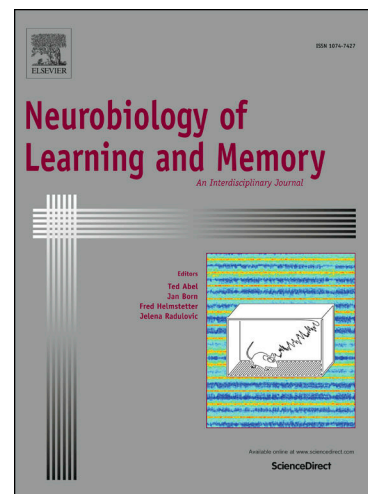
Cross-modal involvement of the primary somatosensory cortex in visual Working Memory: a repetitive TMS study

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ABSTRACT

Recent literature suggests that the primary somatosensory cortex (S1), once thought to be a low-level area only modality-specific, is also involved in higher-level, cross-modal, cognitive functions. In particular, electrophysiological studies have highlighted that the cross-modal activation of this area may also extend to visual Working Memory (WM), being part of a mnemonic network specific for the temporary storage and manipulation of visual information concerning bodies and body-related actions. However, the causal recruitment of S1 in the WM network remains speculation.

In the present study, by taking advantage of repetitive Transcranial Magnetic Stimulation (rTMS), we look for causal evidence that S1 is implicated in the retention of visual stimuli that are salient for this cortical area. To this purpose, in a first experiment, high-frequency (10 Hz) rTMS was delivered over S1 of the right hemisphere, and over two control sites, the right lateral occipital cortex (LOC) and the right dorsolateral prefrontal cortex (dlPFC), during the maintenance phase of a high-load delayed match-to-sample task in which body-related visual stimuli (non-symbolic hand gestures) have to be retained. In a second experiment, the specificity of S1 recruitment was deepened by using a version of the delayed match-to-sample task in which visual stimuli depict geometrical shapes (non-body related stimuli).

Results show that rTMS perturbation of S1 activity leads to an enhancement of participants' performance that is selective for body-related visual stimuli; instead, the stimulation of the right LOC and dlPFC does not affect the temporary storage of body-related visual stimuli. These findings suggest that S1 may be recruited in visual WM when information to store (and recall) is salient for this area, corroborating models which suggest the existence of a dedicated mnemonic system for body-related information in which also somatosensory cortices play a key role, likely thanks to their cross-modal (visuo-tactile) properties.

1. INTRODUCTION

In the last two decades, the role of the primary somatosensory cortex (S1) in high-order cognitive functions has been widely investigated. Studies using different techniques, like functional magnetic resonance imaging (fMRI), electroencephalography (EEG) or non-invasive brain stimulation, showed that S1 is activated not only during the elaboration of afferent somatosensory stimuli and vicarious somatosensation by touch observation, but it is also involved in higher-order cognitive functions such as emotion recognition, motor learning by observation and body representation (e.g., Avenanti, Bolognini, Maravita, & Aglioti, 2007; Blakemore, Bristow, Bird, Frith, & Ward, 2005; Bolognini, Rossetti, Fusaro, Vallar, & Miniussi, 2014; Lametti & Watkins, 2016; McGregor, Cashaback, & Gribble, 2016; Pisoni, Romero Lauro, Vergallito, Maddaluno, & Bolognini, 2018; Pitcher, Garrido, Walsh, & Duchaine, 2008; Rossetti, Miniussi, Maravita, & Bolognini, 2012; Sel, Forster, & Calvo-Merino, 2014; Valchev, Tidoni, Hamilton, Gazzola, & Avenanti, 2017; Zazio, Guidali, Maddaluno, Miniussi, & Bolognini, 2019). The activation of S1 seems to extend also to memory and attention of touch (e.g., Bauer, Oostenveld, Peeters, & Fries, 2006; Forster, Tziraki, & Jones, 2016; Gallace & Spence, 2009; Ku et al., 2015; Papagno, Cecchetto, Pisoni, & Bolognini, 2016; Papagno, Minniti, Mattavelli, Mantovan, & Cecchetto, 2017; Preuschhof, Heekeren, Taskin, Schubert, & Villringer, 2006; Taylor-Clarke, Kennett, & Haggard, 2002; Zhao & Ku, 2018).

In particular, considering the domain of memory, Christophel and Haynes (2014), in an fMRI experiment, showed that the retention of complex visuo-spatial pattern stimuli (i.e., moving dots), besides activating lower-level visual areas and the posterior parietal cortex, also recruited S1. This result would suggest that visual features may be encoded through a cross-modal (visual-tactile) mapping, a process by which S1 takes part into the storage of visual information in working memory (WM) (Christophel & Haynes, 2014). Other clues on the potential cross-modal recruitment of somatosensory cortical areas in visual WM are provided by the studies of Ku and colleagues (2015, 2017, 2018): these authors showed that participants' performance in a tactile-visual delayed match-to-sample task was impaired when single-pulse transcranial magnetic stimulation (TMS) over S1 is delivered 300 ms after the onset of the tactile stimulus. Instead, high-order cortical areas, like the posterior parietal cortex and the dorsolateral prefrontal cortex (dlPFC), were recruited during this cross-modal task at different (longer) timepoints of the mnemonic process. However, in such experiments, the tasks were not purely visual; indeed, the authors adopted cross-modal (tactile-to-visual) WM paradigms requiring to

exchange information between touch and vision (Ku et al., 2015; D. Zhao & Ku, 2018; D. Zhao, Zhou, Bodner, & Ku, 2017).

In addition, there are convergent findings that our brain is equipped with a WM sub-system that is specific for the temporary storage and manipulation of visual information concerning bodies and body-related actions (Galvez-Pol, Forster, & Calvo-Merino, 2020; Rumiati & Tessari, 2002; Shen, Gao, Ding, Zhou, & Huang, 2014; Smyth, Pearson, & Pendleton, 1988; Smyth & Pendleton, 1989; Wood, 2007). The neural underpinnings of this visual 'body-related' memory system comprise a complex network of cerebral areas including specialized visual regions, such as the fusiform gyrus and the extrastriate body area (Peelen & Downing, 2005; Urgesi, Candidi, Ionta, & Aglioti, 2007), premotor and tempo-parietal regions related to the action observation network (Cai et al., 2018; Liu, Lu, Wu, Shen, & Gao, 2019; Lu et al., 2016), but also 'low-level' somatosensory and motor areas (Arslanova, Galvez-Pol, Calvo-Merino, & Forster, 2019; Galvez-Pol, Calvo-Merino, Capilla, & Forster, 2018; Galvez-Pol, Forster, & Calvo-Merino, 2018). Overall, this memory network strongly overlaps the ones implicated in the processing of our own body and motor representations (Longo, Azañón, & Haggard, 2010; Molenberghs, Cunnington, & Mattingley, 2012). The role of S1 in this WM sub-system has been recently highlighted in an EEG study showing that *contralateral delayed activity* (CDA), a neurophysiological marker of WM (for a review, see: Luria, Balaban, Awh, & Vogel, 2016), increased in left and right somatosensory cortices selectively during the maintenance of visual body-related stimuli (i.e., non-symbolic hand gestures); moreover, the magnitude of this increase was correlated with the number of stimuli to memorize (Galvez-Pol, Calvo-Merino, et al., 2018).

Despite these recent findings, no study has investigated the causal involvement of S1 in visual WM so far. To this aim, we have run a TMS study to obtain the first causal evidence of the actual recruitment of S1 during a visual body-related WM task. Indeed, as repetitive TMS (rTMS) allows to prove the causal relationship between the stimulated cortical area and its involvement in a cognitive function (Bolognini & Ro, 2010), we applied this technique 'online' to interfere with S1 functioning while participants performed a WM task, i.e., delayed match-to-sample task (e.g., Galvez-Pol, Calvo-Merino, et al., 2018; Vogel & Machizawa, 2004; Vogel, McCollough, & Machizawa, 2005) where the visual stimuli to memorize depicted body-related information (hand gestures – *Experiment 1*). If S1 is recruited for processing bodily stimuli during visual WM tasks, then the perturbation of its activity should affect participants' performance when rTMS is delivered at a

timepoint corresponding to the maintenance phase of the mnemonic process. Following the evidence that higher memory loads lead to a greater CDA in the electrodes overlapping somatosensory cortices (Galvez-Pol, Calvo-Merino, et al., 2018), we decided to use an experimental task with a high number of visual body-related stimuli to memorize (Luck & Vogel, 2013). We chose S1 of the right hemisphere, following Baddeley's model (2000) proposing that visual WM is mainly represented in the right hemisphere (Baddeley, 2000), as well as evidence of a right hemisphere dominance for touch observation (e.g., Blakemore et al., 2005; Bolognini, Rossetti, Convento, & Vallar, 2013) and body representation (e.g., Longo et al., 2010; Tsakiris, Hesse, Boy, Haggard, & Fink, 2007).

Two cortical areas of the right hemisphere were also targeted with TMS: the lateral occipital cortex (LOC) and dlPFC. In our starting hypothesis, the right LOC should act as a control site; this extrastriate area is implicated in the feature-based analysis of visual information (e.g., Amedi, Malach, Hendler, Peled, & Zohary, 2001; Grill-Spector, Kourtzi, & Kanwisher, 2001; Kourtzi & Kanwisher, 2001; Malach et al., 1995) but its role in the processing and the possible storing of body-related visual stimuli still needs to be determined (Gayet, Paffen, & Van der Stigchel, 2018; Heuer, Schubö, & Crawford, 2016; Pitcher, Charles, Devlin, Walsh, & Duchaine, 2009; Xu, 2018; Xu & Chun, 2006). Conversely, the dlPFC was chosen according to a recent proposal that visual WM storage does not rely on sensory processing areas, but rather on specialized frontal (and parietal) areas not involved in low-level sensory processing per se (such as S1) (Xu, 2017). The right dlPFC is considered a key node of the WM network; indeed, recent studies suggest that its activation is related to the manipulation of stored information rather than to their maintenance (e.g., Barbey, Koenigs, & Grafman, 2013; C. Kim, Kroger, Calhoun, & Clark, 2015; Postle et al., 2006; Rowe, Toni, Josephs, Frackowiak, & Passingham, 2002; Veltman, Rombouts, & Dolan, 2003). However, previous TMS studies, where both the right and left dlPFC were stimulated, not always were successful in modulating participants' performance during either visual and non-visual WM tasks (e.g., Bagherzadeh, Khorrami, Zarrindast, Shariat, & Pantazis, 2016; Beynel et al., 2019; Chung, Rogasch, Hoy, & Fitzgerald, 2018; Hamidi, Tononi, & Postle, 2009). Hence, by stimulating LOC and dlPFC of the right hemisphere, we aimed at verifying the causal involvement of S1 in WM, assessing its main role in processing visual body-related stimuli (at variance with LOC) and in their storage (at variance with dlPFC); this would offer a better comprehension of its role in visual WM as compared to other areas of the same network: by targeting two other functionally relevant areas, our study provides

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stronger clues on the functional selectivity of S1 in visual WM tasks, rather than simply controlling for sensory and placebo rTMS confounds, as it would have happened if we had used a sham stimulation or a functionally 'neutral' area (such as the vertex) (Duecker & Sack, 2015).

In the second experiment (*Experiment 2*), we further explored the selective recruitment of the right S1 for body-related visual stimuli by assessing the effect of S1 rTMS on a delayed match-to-sample task depicting geometric shapes; we expected no effect of rTMS over S1 if visual stimuli are not body-related (e.g., Galvez-Pol, Calvo-Merino, et al., 2018).

2. MATERIALS and METHODS

2.1. Participants

Forty healthy male and female volunteers were initially recruited, 20 for each experiment. Two participants in *Experiment 1* and one in *Experiment 2* were then excluded because their averaged accuracy in the experimental tasks without rTMS was below chance level (< 50%), while one participant of *Experiment 2* dropped out before having completed all the experimental sessions, leaving thus the final analyzed sample to 18 participants in each experiment (*Experiment 1*: 4 males, mean age ± standard deviation – S.D.= 23.6 ± 2.7, mean education ± S.D.= 15.4 ± 2.1; *Experiment 2*: 9 males, mean age ± S.D.= 23.7 ± 2.3, mean education ± S.D.= 15.5 ± 1.8). *A-priori* estimation of the sample size by using the software G*Power suggested the need of a sample of at least 17 participants (i.e., effect size $F = .3$; alpha error level: $p = .05$; statistical power = .80, actual power = .81) (Faul, Erdfelder, Buchner, & Lang, 2009).

All subjects were right-handed accordingly to the Edinburgh Inventory (Oldfield, 1971); exclusion criteria included a history of peripheral sensory disorders and/or central neurological and psychiatric diseases, and contraindications to TMS (among which: familiarity with epilepsy, assumption of neuroleptic drugs, pregnancy state; Rossi, Hallett, Rossini, & Pascual-Leone, 2009). All subjects were naive to the purpose of the study; every participant took part in only one of the two experiments. Before undergoing the experiment, all of them gave their written informed consent. Participants received European University Credits (ECTS; 0.1 ECTS for 30 min of experiment) for their participation. The protocol was performed following the ethical standards of the Declaration of Helsinki and was approved by the Ethical Committee of the University of Milano-Bicocca.

2.2. Delayed match-to-sample task

The delayed match-to-sample task adopted in the two experiments was adapted from previous studies (e.g., Galvez-Pol, Calvo-Merino, et al., 2018; Galvez-Pol, Forster, et al., 2018; Vogel & Machizawa, 2004). The set of six grey-scaled hand gestures (not having any meaning or symbolism) presented in *Experiment 1* (dimension: 1.2° X 2.4° of visual angle) was the same used by Galvez-Pol and colleagues (2018a, b). Geometric shapes in *Experiment 2* were obtained from the outline of hand gestures and were matched for dimension and scale of color **(Figure 1a)**.

During the task, participants sat comfortably on a chair in a slightly lit room in front of a PC screen placed at a distance of 57 cm. Each trial started with a frame (dimension: 10° X 10°) in which a fixation cross appeared on a white background with a duration jittered between 5500 and 6000 ms ('fixation cross' frame). This first frame was followed by one depicting a black arrow over the fixation cross pointing to the hemifield (i.e., right or left) in which the arrays would appear (duration: 200 ms). Participants were instructed to always look at the fixation cross and not move their eyes in the direction indicated; they could use the arrow as a clue and focus their attention on a specific hemifield. As soon as the attentional arrow disappeared, a second "fixation cross" frame was presented (duration: 800 ms). Then, the 'memory' array appeared for just 200 ms followed by a frame depicting only the fixation cross ('maintenance phase', duration: 1000 ms) and, then, the 'test' array appeared. The test array remained on the screen until participants pressed one of the keys of the mouse with his/her right hand **(Figure 1b)**. If the stimuli presented in 'memory' and 'test' arrays were the same, participants were instructed to press, as fast as possible, the left key of the mouse; conversely, if they were different, the right key had to be pressed. The 'test' arrays could differ for just 1 of the 3 stimuli presented in the 'memory' arrays. During the task, stimuli were presented in fixed positions (i.e., 1 stimulus in the upper side, 1 central and 1 in the lower side of the array) and the arrays appeared randomly in the right or left hemifield. All stimuli arrays were presented within two 5° X 10° rectangular regions that were centered 2.5° to the left and right of the fixation cross. The distance (center to center) between stimuli within a hemifield was 2.8°.

Three stimuli per array were selected according to previous literature that highlighted how a delayed match-to-sample task with such several stimuli had a high memory load (Luck & Vogel, 2013; Luria et al., 2016). A pilot study was conducted on 10 participants to verify the difficulty of the task: results showed that with 3-

stimuli arrays, the average accuracy was of about 65%; conversely, when the task was easier (2-stimuli arrays), it was above 85%, while, when the task was harder (4-stimuli arrays), it was at chance level (i.e., 50%).

During the task, a total of 64 couple of arrays was presented: in 32 of them, there were no differences between 'memory' and 'test' arrays ('same' trials) while in the other half the two differed ('different' trials). For every trial condition ('same' or 'different'), 16 trials showed stimuli lateralized to the left hemifield and 16 to the right one. For 'different' trials, the position of the different stimulus in the array was balanced between the two hemifields. In every testing session and for every participant, trials were presented in a randomized order. Overall, the task lasted about 12 minutes. All 64 'memory' arrays were unique and the same composition of visual stimuli was never presented twice during a single task. In *Experiment 1*, half of the arrays depicted gestures made with the left hand while the other half gestures made with the right hand (balanced for every trial condition). These conditions were applied equally to both experiments; the only difference between the two relied on the stimuli depicted in the arrays (i.e. hand gestures in *Experiment 1* and geometric shapes in *Experiment 2*).

In every session, the delayed match-to-sample task was administered twice: with and without rTMS. rTMS was delivered online during the 'maintenance phase' of the task, namely, 200 ms after the disappearing of the 'memory' array. This timepoint was selected according to previous neurophysiological evidence that CDA, the neurophysiological marker of the WM retention phase, starts over somatosensory cortices at this timing after the disappearing of the stimulus to memorize (e.g., Galvez-Pol, Calvo-Merino, et al., 2018), hence following the earlier perceptual processing stage of the visual stimuli (e.g., Koivisto, Henriksson, Revonsuo, & Railo, 2012; Mullin & Steeves, 2011).

Before starting each experimental session, a brief version of the task (10-trials) was administered to participants as a training.

Trials randomization and timing of the frames were presented under computer control using the software E-Prime (version 2.0, Psychology Software Tool, Inc.).

2.3. Repetitive Transcranial Magnetic Stimulation (rTMS)

High-frequency (10 Hz) rTMS was delivered online, during the task, in the two experiments. rTMS was delivered using a biphasic Magstim Super Rapid 2 stimulator and a figure-of-eight coil (diameter=70 mm;

Magstim, Whitland, UK). Stimulation lasted for 300 ms (i.e. 3 pulses) and, for every participant, the intensity was fixed, set at 60% of the maximum stimulator output (e.g., Bolognini & Ro, 2010; Robertson, Théoret, & Pascual-Leone, 2003). These parameters were selected according to previous literature showing its efficacy for influencing performance in WM tasks (e.g., Bona, Herbert, Toneatto, Silvanto, & Cattaneo, 2014; Cattaneo et al., 2015; Cattaneo, Pisoni, Papagno, & Silvanto, 2011; Cohen Kadosh et al., 2007; Heuer et al., 2016; Mullin & Steeves, 2011; Pitcher et al., 2009; Silvanto, Schwarzkopf, Gilaie-Dotan, & Rees, 2010). A total of 192 pulses (3 pulses x 64 trials) was delivered in each experimental session.

We localized the targeted areas (**Figure 1c)** using the neuronavigation software SoftAxic Optic 2.0 (E.M.S., Bologna, Italy, ww.softaxic.com; see, for instance, Giurgola, Pisoni, Maravita, Vallar, & Bolognini, 2019; Guidali, Pisoni, Bolognini, & Papagno, 2019 for a similar procedure) and reconstructing a virtual volume of each participant's brain. This software allows creating a magnetic resonance image (MRI) of the cerebral cortex in Talairach coordinates from a template through a warping procedure. Parameters for warping the template image are estimated on the basis of four digitized skull landmarks (i.e., nasion, inion, and the right/left preauricular points), and 60 uniformly distributed points mapped on the participant's scalp, with a mean error of 2.11 mm and a standard deviation of 2.04 mm. Digitalization and neuronavigation were achieved via a graphic user interface and a 3D optical digitizer (NDI, Polaris Vicra). For each participant, the location of S1 was identified following the Talairach coordinates X = 47, Y = -32, Z = 57 on the MRI template and using a 3D virtual reconstruction of the participant's brain. The S1 coordinates were derived from fMRI studies (Boakye, Huckins, Szeverenyi, Taskey, & Hodge, 2000). Importantly, previous TMS studies using similar coordinates to stimulate S1 found related functional effects like the induction of tactile extinction or paresthesia (e.g., Bolognini, Papagno, Moroni, & Maravita, 2010; Bolognini et al., 2014). The stimulation site on the scalp corresponding to the right S1 was also localized by using an additional anatomical criterium consisting in moving the coil 2 cm posterior from the left-hand motor hotspot (i.e., right primary motor cortex), as previously done in some studies stimulating S1 (e.g., Avenanti et al., 2007; Fiorio & Haggard, 2005; Giurgola et al., 2019; Zazio et al., 2019).

The left-hand motor hotspot and participants' resting motor threshold (rMT) were determined by calculating the minimum stimulator output able to elicit visually detectable motor twitches in the contralateral left hand (with particular attention to the *first dorsal interosseus* muscle) 3 times out of 5 while right M1 was stimulated

(Rossi et al., 2009). Mean rMT was of (mean ± S.D.) 61 ± 5.8% in *Experiment 1* and 58.5 ± 7.7% in *Experiment 2*. Additionally, we further checked to not stimulating M1, few TMS pulses were delivered over the S1 scalp location to determine whether its stimulation could induce movements in the left hand; none of the participants showed detectable motor twitches when TMS was applied to S1 with the intensity used during the experiment (i.e. at 60% of the maximum stimulator output, see above).

In *Experiment 1*, the same neuronavigation procedure was used to localize LOC and dlPFC: mean Talairach coordinates of right LOC (X = 41, Y = -72, Z = 4) and right dlPFC (X = 42, Y = 28, Z = 26) were taken from previous rTMS and fMRI studies using similar tasks (Daniel, Katz, & Robinson, 2016; Xu & Chun, 2006). During S1 and dlPFC stimulation, the coil was placed tangentially to the scalp with the handle hold backward and laterally at a 45° angle to the sagittal plane (e.g., Bagherzadeh et al., 2016; Orth & Rothwell, 2004); during LOC stimulation, the coil handle pointed upwards, parallel to the midline (e.g., Pitcher et al., 2009; Silvanto et al., 2010). Throughout the experiment, the correct and stable position of the coil was then monitored on-line with the same neuronavigation system.

------------------ Insert Figure 1 here ----------------

2.4. Experimental procedure

The study took place in the TMS laboratory of the Department of Psychology of the University of Milano-Bicocca. Experimental procedure and setting were the same in both experiments, what differed was the number of sessions in which participants had to take part. *Experiment 1* comprised 3 sessions differing only for the cortical area stimulated with rTMS during the experimental task (i.e., S1, LOC, and dlPFC). The order of the 3 sessions was randomized and counterbalanced among participants. *Experiment 2* comprised 1 session in which the only S1 was stimulated.

In both experiments, during the first session, the informed consent, the Edinburgh Inventory, and the TMS safety checklist questionnaire were administered to the participants. At the beginning of every session, participants underwent training with the delayed match-to-sample task to familiarize themselves with it. In each session, the delayed match-to-sample task was administered twice, without (baseline) and with rTMS (15 minutes inter-tasks break); the order of these two conditions was kept fixed within the experimental sessions

but randomized between participants. Before administering the task with rTMS, the neuronavigation procedures were carried out. Each rTMS session lasted approximately 60 minutes and, in *Experiment 1*, an interval of at least 24 hours separated one session from the other.

At the end of both experiments, participants were informally inquired about their perception of experimental visual stimuli. In *Experiment 1*, all participants reported that the viewed visual stimuli represented human hand gestures. In *Experiment 2* participants defined the visual stimuli as 'geometric' or 'meaningless' shapes/figures; importantly, nobody described them as 'human hands'.

2.5. Statistical analysis

In both experiments, participants' performance in the delayed match-to-sample task was analyzed accordingly to Signal Detection theory (Green & Swets, 1966). Signal detection measures have the advantage of allowing for the separation of perceptual level and decision level by assessing the contribution of stimulus-related (i.e., perceptual sensitivity, *d'*) and subject-related (i.e., response bias, *c*) influences on performance: the *d'* parameter reflects the subject's accuracy to discern a sensory event from its background (perceptual sensitivity), while the *c* parameter reflects the subject's decision criterion of response (response bias).

In *Experiment 1*, baseline performance in the 3 sessions was compared through a 1-way ANOVA with Session (S1, LOC, dlPFC) as the main within-subjects factor. Given the absence of difference between baselines ($F_{2,34}$ = .99, p = .38, η^2_p = .055), to simplify the model, the 3 baselines were mediated and a repeated measures ANOVA (rmANOVA) with within-subjects factors Session (Baseline, S1-rTMS, LOC-rTMS, dlPFC-rTMS) and Hemifield (right, left, according to the side of visual stimuli presentation in the task's trials) was performed on *d'* and *c* values. In *Experiment 2*, a similar Session (Baseline, S1-rTMS) X Hemifield (left, right) rmANOVA was run. Statistical significance was set at *p*-values < .05. The Shapiro-Wilks test confirmed the normality of the distributions and when data sphericity was not confirmed by Mauchly's test, the Greenhouse-Geisser correction was applied. Significant main effects were further explored with post-hoc comparisons using t-tests and applying the Bonferroni correction for multiple comparisons. As effect size values, partial eta-squared (η^2_p) was calculated in every rmANOVA, and Cohen's *d* was reported in post-hoc tests. For each variable, the mean ± standard error (S.E.) is reported. Statistical analyses were performed using the software Jamovi (version 1.1.9, the Jamovi project, www.jamovi.org)

3. RESULTS

3.1. *Experiment 1*

With respect to perceptual sensitivity (*d'*), results showed a main effect of factor Session ($F_{3,51}$ = 5.74, *p* = .009, η^2_p = .251) but neither of factor Hemifield ($F_{3,51}$ = .002, *p* = .96, η^2_p < .001) nor their interaction ($F_{3,51}$ = .89, *p* = .451, η^2_p = .05), suggesting a modulation of participants' performance independently of the stimulated hemifield. Hence, statistical significance of factor Session was further explored with post-hoc comparisons which highlighted that the stimulation of S1 enhanced participants' performance (*d'* = 1.23 ± .1) with respect to all other conditions (*vs.* baseline = .95 ± .09, t = 2.92, *p* = .021, Cohen's *d* = .72; *vs.* LOC-rTMS = .94 ± .09, t = 2.93, *p* = .021, Cohen's *d* = .72; *vs.* dlPFC-rTMS = .85 ± .11, t = 3.9, *p* = .002, Cohen's *d* = .89; **Figure 2a**). The analysis of the response bias (*c*) showed no significant effects of Session ($F_{3,51}$ = 2.35, *p* = .083, η^2_p = .12), Hemifield ($F_{3,51}$ < .01, *p* = .99, η^2_p < .01) and of their interaction ($F_{3,51}$ = .22, *p* = .883, η^2_p = .01; **Figure 2a**), suggesting that the modulation of performance found was not due to a different way in which participants tended to respond at the experimental task in the different conditions.

3.2. *Experiment 2*

In *Experiment 2*, rmANOVA on *d'* values showed no significant effects of all main factors and interactions (Session: $F_{1,17}$ = 1.01, *p* = .33, η^2_p = .06; Hemifield: $F_{1,17}$ = .61, *p* = .445, η^2_p = .04; Session X Hemifield: $F_{1,17}$ = .67, *p* = .416, η^2_p = .04; **Figure 2b**), hence rTMS over S1 was not effective when the visual stimuli depicted geometric shapes. Similarly, the rmANOVA on *c* values showed no effects (Session: $F_{1,17}$ = 2.29, *p* = .149, η^2_p = .12; Hemifield: $F_{1,17}$ = .83, *p* = .375, η^2_p = .05; Session X Hemifield: $F_{1,17}$ = .3, *p* = .594, η^2_p = .02; **Figure 2b**).

We also run an explorative independent-samples t-test to compare the baseline performance in *Experiments 1* and *2*, which showed no significant differences suggesting that the two tasks have a similar difficulty and participants tend to respond with the same criterion (*d'*: t_{34} = .51, *p* = .617, Cohen's *d* = .17; *c*: t_{34} = -.93, *p* = .357, Cohen's *d* = -.31). A second, explorative, independent-samples t-test was run to compare participants performance during S1-rTMS in the two experiments: as expected, *d'* values differed between *Experiment 1* and *2* (t_{34} = 1.79, *p* = .042, Cohen's *d* = .6) while *c* did not (t_{34} = .9, *p* = .373, Cohen's *d* = -.3).

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Finally, in both experiments, we also checked whether the participant's sex may have influenced our findings, given the difference in the number of males and females in the two experiments (indeed, *Experiment 1* comprised 4 males and 14 females, while 9 male and 9 females took part to *Experiment 2*). To this aim we run two additional rmANOVAs (one for each experiment) with the between-subjects factor Sex. In both experiments, Sex (*Experiment 1*: $F_{3,48} = 1.27$, $p = .276$, $\eta^2_p = .07$; *Experiment 2*: $F_{1,16} = .01$, $p = .913$, $\eta^2_p < .01$) and the interaction Session X Sex (*Experiment 1*: $F_{3,48} = .65$, $p = .585$, $\eta^2_p = .04$; *Experiment 2*: $F_{1,16} < .01$, $p = .995$, $\eta^2_p < .01$) did not attain the significance level, excluding the influence of sex differences in the two experiments.

---------------- Insert Figure 2 here -----------------

4. DISCUSSION

The present study has investigated whether S1 is causally involved in the maintenance of body-related information (i.e., hand gestures) in visual WM. We have found that participants' performance in a delayed match-to-sample task visually presenting hand gestures to-be-remembered is enhanced by high-frequency rTMS delivered over the right S1. Importantly, this enhancement effect is area- and stimulus-specific: indeed, when rTMS is delivered over the right LOC or the right dlPFC (*Experiment 1*), or when the task shows visual stimuli that are not body-related (geometrical shapes – *Experiment 2*), rTMS is ineffective. At the same time, the enhancement of performance during S1 stimulation is independent of the hemifield of visual presentation (and thus from the activated hemisphere). Overall, our findings provide novel evidence about the cross-modal recruitment of S1 by visual WM, highlighting its role not only for perceiving bodily sensation but also for encoding and maintaining visual bodily information in memory.

The present results show the existence, in the human WM network, of a sub-system that is specific for visual body-related stimuli (Galvez-Pol, Forster, et al., 2020), where S1 represents an important node. Our findings extend the conclusions of recent EEG studies: by using a subtractive event-related potentials method (Galvez-Pol, Calvo-Merino, & Forster, 2020), Galvez-Pol and colleagues (2018a, b) found that primary somatosensory and motor cortices are recruited during the maintenance phase of a visual WM task where body-related information had to be retained (Galvez-Pol, Calvo-Merino, et al., 2018; Galvez-Pol, Forster, et al., 2018).

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However, EEG suffers from low spatial resolution and the causal relationship between the activation of a specific primary sensory area and the recorded signal (i.e., CDA) in the overlapping electrodes cannot be fully ruled out. Thus, the involvement of S1 remained speculation. By taking advantage of rTMS, the results of the present study provide the first causal evidence of S1 involvement in visual WM.

Nowadays, there are convergent findings that alpha-band neuronal oscillations with a frequency of about 10 Hz (i.e. the same frequency of our rTMS protocol) are fundamental for WM coding and storage, likely through the suppression of distracting information (e.g., Bonnefond & Jensen, 2012; Foster, Bsales, Jaffe, & Awh, 2017; Foster, Sutterer, Serences, Vogel, & Awh, 2015; Jensen, Gelfand, Kounios, & Lisma, 2002; Leiberg, Lutzenberger, & Kaiser, 2006; Roux & Uhlhaas, 2014). Furthermore, online rTMS can enhance cognitive performance when is delivered with this frequency (e.g., Emrich, Johnson, Sutterer, & Postle, 2017; Heuer et al., 2016; Klimesch, Sauseng, & Gerloff, 2003; Luber & Lisanby, 2014; Preston, Anderson, Silva, Goldberg, & Wassermann, 2010). Accordingly, we have found that 10 Hz rTMS induces a facilitatory effect during the visual WM task, leading to behavioral enhancement, which may be the result of enhanced synchronization of visuo-tactile responses in S1 by rTMS, transiently entraining them to an alpha band-like frequency (Thut & Miniussi, 2009; Thut et al., 2011). The delivery of high-frequency rTMS might have acted by transiently entraining visuo-tactile S1 neurons to the correct, alpha-like, brain rhythm, leading to better retention of visual information pertaining to the body. An alternative hypothesis to explain the performance enhancement brought about by high-frequency rTMS over S1 could be that, under normal conditions, the cross-modal recruitment of S1 might exert a sort of inhibitory influence on visual WM. If this is the case, rTMS, by perturbating S1 activity, would reduce such inhibitory drive allowing a better retention of the information. Both these interpretations remain at a speculation level since we could only conjecture on the direction of the rTMS effects (inhibition vs facilitation); at this level, we have only obtained evidence of the causal involvement of S1 in visual WM for hand gestures.

The S1 specificity in WM-related processing is highlighted by the results from *Experiment 2* that show that S1 is not recruited during a visual WM task if geometric shapes have to be memorized. Hence, we speculate that S1 plays a role in WM thanks to its cross-modal properties which are helpful to enhance the computational – and, thus, the maintenance – capacity of the memory network, especially when the task is difficult (as the present). This proposal is supported by neurophysiological evidence that CDA over somatosensory cortices is

greater when the number of body-related stimuli to memorize is high (Galvez-Pol, Calvo-Merino, et al., 2018) and alpha-band oscillations (and synchronization) increase with the memory load (Jensen et al., 2002; Leiberg et al., 2006).

Another interesting finding is that the visual functions of S1 are not related to the hemifield of visual stimuli presentation. Previous evidence indicated that CDA is recorded only over somatosensory cortices contralateral to the hemifield of visual stimuli presentation (Arslanova et al., 2019; Galvez-Pol, Calvo-Merino, et al., 2018), which has led to suggest that the somatosensory cortex is mainly activated by stimuli processed by the ipsilateral visual cortices. The present findings lead us to hypothesize that the activation of the S1 during the maintenance phase, at least in the right hemisphere that seems to have a special role in touch observation (e.g., Bolognini et al., 2013), may influence visual processing for memory functions regardless of the hemifield lateralization of the visual information; hence, S1 would be involved in both intra- and inter-hemispheric processing of body-related visual information. However, future studies are needed to further explore the contribution of the left S1 in order to clarify the hemifield selectivity of S1 for visual processing and its hemispheric dominance for WM-related functions.

The timing of rTMS delivery provides a further reflection on the phase of S1 recruitment in WM. In the present work, rTMS was applied over S1 200 ms after the offset of the visual stimuli to be remembered. We have chosen this timing following previous evidence highlighting that the time-course of the maintenance phase (CDA) in delayed match-to-sample visual tasks starts at this timepoint after the visual elaboration of the stimuli (e.g., Galvez-Pol, Calvo-Merino, et al., 2018; Vogel & Machizawa, 2004; Vogel et al., 2005). Likely, S1 might be activated also during the encoding, and maybe the recalling phases of the mnemonic process.

The results of *Experiment 1* also show that the perturbation of right LOC and right dlPFC does not modulate participants' performance in our delayed match-to-sample task. Considering LOC, previous works in the field of the '*sensory recruitment*' models of WM (D'Esposito & Postle, 2015) showed that the activation of extrastriate areas participates to visual WM, beyond the low-level visual processing (e.g., Cattaneo et al., 2011; Harrison & Tong, 2009; Parra, Della Sala, Logie, & Morcom, 2014; Song & Jiang, 2006; Y. Zhao, Kuai, Zanto, & Ku, 2020). Even if these models are still debated (for a review, see: Xu, 2017), studies that applied rTMS over LOC found a modulation of participants' performance in visual WM tasks after or during its stimulation (Bona et al., 2014; Heuer et al., 2016; Mullin & Steeves, 2011, 2013; Romei, Gross, & Thut, 2010).

Independently from the direction (excitatory/inhibitory) of rTMS effects, in all the previous works, the visual stimuli to process and retain depicted simple geometric shapes, like dots or squares, or objects, but not body-related visual stimuli. Both neuroimaging and non-invasive brain stimulation studies reported that LOC is active selectively during the visual processing and the retention of non-biological objects (e.g., Heuer et al., 2016; J. G. Kim, Biederman, & Juan, 2011; Mullin & Steeves, 2011; Myers, Walther, Wallis, Stokes, & Nobre, 2015). For instance, Pitcher and colleagues (2009) showed that rTMS over the right LOC impairs object recognition; visual recognition of faces and bodies was impaired by stimulating the right occipital face area and the right extrastriate body area, respectively (Pitcher et al., 2009). Hence, our findings provide further support that LOC is not specialized for body-related stimuli.

The absence of modulation during right dlPFC stimulation can be explained considering that, within the WM network, this area is fundamental for the manipulation of stored information (Baddeley, 2012) and we delivered rTMS while participants have to simply retain the stored visual information rather than manipulating it. In line with the present results, previous rTMS studies did not find any significant modulation of participants' performance when TMS was delivered over the right dlPFC during the maintenance phase of a memory task (e.g., Hamidi, Tononi, & Postle, 2008; Hamidi et al., 2009; Luber et al., 2007; Postle et al., 2006; Rossi et al., 2011, 2006). Conversely, two recent high-frequency rTMS studies, investigating the effects of dlPFC stimulation on WM functions, found a modulation of participants' performance selectively during high-load WM tasks in which the manipulation of stored information is essential (i.e., delayed response alphabetization task and spatial 3-back task) (Bakulin et al., 2020; Beynel et al., 2019). Again, studies using fMRI and near-infrared spectroscopy highlighted that right dlPFC activation is greater during backward span tasks, which required manipulation of the stored information, rather than forward ones, which instead required maintenance (Gerton et al., 2004; Hoshi et al., 2000). Overall, these findings are consistent with the hypothesis that the role of dlPFC is not the storage of information in WM itself, rather this area is crucial for stimuli manipulation and control of their retention in other brain areas (Baddeley, 2012). Hence, we suggest that the absence of effects in the present study is mainly due to the timing at which rTMS is delivered (i.e., during the maintenance phase) and the intrinsic characteristics of the used WM task.

The present study suffers from some methodological limitations that need to be taken into consideration. First of all, we cannot exclude that S1-rTMS effects may have widespread to the nearby secondary somatosensory

cortex, which could also be involved in the retention of body-related information, especially considering that also this area has neurons with visuo-tactile properties (e.g., Keysers et al., 2004; Schaefer, Heinze, & Rotte, 2012; Schaefer, Xu, Flor, & Cohen, 2009; Sun, Welchman, Chang, & Di Luca, 2016). At the same time, the use of a standardized template to found target cortical areas, instead of individual MRIs, might have reduced the precision of the stimulation. However, the adopted neuronavigation procedure has been successfully used in previous studies to localize (and stimulate) focal areas like the ones of our study with precision within few mm (e.g., Bolognini, Rossetti, Maravita, & Miniussi, 2011; Carducci & Brusco, 2012; Collins & Jacquet, 2018; Guidali et al., 2019; Rossi et al., 2011) and thus we can assume to have targeted the correct brain regions. Furthermore, the use of the same fixed intensity for all participants, an approach commonly used to stimulate nonmotor areas, could have led to under- or over-stimulate some participants (Bolognini & Ro, 2010; Robertson et al., 2003). The ideal determination of the stimulation intensity would require the estimation of the TMS-induced electric field in the different targeted areas, overcoming individual differences in scalp-to-cortex distance of different brain regions (Janssen, Oostendorp, & Stegeman, 2014).

A final note: since *Experiment 2* aimed solely at verifying the stimulus-selectivity of S1 for the maintenance of hand gesture stimuli, we did not assess the selective involvement of other cortical sites, such as extrastriate areas of the ventral stream (including LOC) or the inferior parietal sulcus, for the maintenance of geometric visual stimuli during WM, as previously demonstrated in other studies (e.g., Parra et al., 2014; Pitcher et al., 2009; Todd & Marois, 2004; Xu & Chun, 2006).

In conclusion, the present work demonstrates the causal, cross-modal, involvement of S1 in a visual WM task where body-related stimuli are depicted, showing the higher-order recruitment of such primary area. This evidence corroborates WM models speculating the existence of a dedicated mnemonic sub-system for body-related information in which cortical regions underpinning the representation of one's body in the brain play a key role, likely through the mediation of cross-modal processes (Galvez-Pol, Forster, et al., 2020). Accordingly, the results of our study suggest that the visuo-tactile properties of S1 might be helpful to enhance the computational capacity of such WM system, especially when a mnemonic process is particularly difficult and additional cognitive resources are required.

FIGURE CAPTIONS

Figure 1. a) Set of hand gestures and related geometrical shapes used in *Experiments 1* and *2* respectively. Stimuli are taken from Galvez-Pol et al. (2018a). **b)** Delayed match-to-sample task used in the two experiments of the study. Three rTMS pulses at a frequency of 10 Hz are delivered 200 ms from the offset of the 'memory' array. **c)** Lateral view of a 3-D brain reconstruction showing the localization of the 3 rTMS sites of *Experiment 1*. In *Experiment 2*, only right S1 was stimulated.

Figure 2. Results of *Experiment 1* **(a)** and *Experiment 2* **(b)**. Left panel: d prime (*d'*); right panel: response bias (*c*). Bonferroni correction for multiple comparisons was applied. * = p < .05; ** = p < .01. Error bars = S.E.

Declaration of interests

The authors declare no competing interest.

Data statement

Acknowledgment

CRediT authorship

Giacomo Guidali: conceptualization, methodology, investigation, data curation, formal analyses, writing – original draft. **Camilla Roncoroni:** methodology, investigation, data curation, formal analyses, writing – review and editing. **Costanza Papagno:** methodology, writing – review and editing. **Nadia Bolognini:** conceptualization, methodology, supervision, writing – original draft.

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Cross-modal involvement of the primary somatosensory cortex in visual Working Memory: a repetitive TMS study

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