CORTEX 119 (2019) 89–99

Available online at www.sciencedirect.com

ScienceDirect

Journal homepage: www.elsevier.com/locate/cortex

Research Report

# Keeping order in the brain: The supramarginal gyrus and serial order in short-term memory

*Giacomo Guidali*[a,b], *Alberto Pisoni*[a], *Nadia Bolognini*[a,c] and *Costanza Papagno*[a,d,*]

[a] *Department of Psychology & Milan Center for Neuroscience - NeuroMI, University of Milano-Bicocca, Milan, Italy*
[b] *Ph.D. program in Neuroscience, School of Medicine and Surgery, University of Milano-Bicocca, Monza, Italy*
[c] *Laboratory of Neuropsychology, IRCCS Istituto Auxologico Italiano, Milan, Italy*
[d] *CIMeC & CeRiN, University of Trento, Rovereto, Italy*

ARTICLE INFO

*Article history:*
Received 13 December 2018
Reviewed 5 February 2019
Revised 22 February 2019
Accepted 10 April 2019
Action editor Eric Wassermann
Published online 20 April 2019

*Keywords:*
Short-term memory
Serial order
Transcranial magnetic stimulation
Supramarginal gyrus
Inferior frontal gyrus

ABSTRACT

A wide range of human activities are performed sequentially in few seconds. We need to maintain a correct temporal order of words in language, movements in actions, directions in navigation, etc. Therefore, it is plausible, in a more economical perspective, that our brain is equipped with a dedicated mechanism for storing a temporal sequence for a short time. To investigate it, we run four TMS experiments, in which participants performed different short-term memory tasks, i.e., three (verbal, spatial, motor) requiring maintenance of an ordered sequence and one (visual) of a static pattern. We demonstrated, for the first time, that the left supramarginal gyrus is one of the key nodes of the STM network involved in retaining an abstract representation of serial order information, independently from the content information, namely the nature of the item to be remembered, which instead is stored separately.

## 1. Introduction

Retention of serial order, namely the ability of detecting and retaining the temporal sequence of incoming information, is a crucial human ability that subtends a wide range of verbal and nonverbal activities, as suggested by the consequences of its impairment in language (e.g., conduction aphasia) and motor (e.g., ideomotor apraxia) domains. As Baddeley (2012) suggests, it is likely that "*evolution has applied the same solution to a problem, maintaining serial order, that crops up in a range of different domains*". If this is the case, it is plausible to assume that our brain could be equipped with a dedicated mechanism

---

* *Corresponding author*. Department of Psychology & Milan Center for Neuroscience - NeuroMI, University of Milano-Bicocca, Milan, Italy.
E-mail addresses: costanza.papagno@unitn.it, costanza.papagno@gmail.com (C. Papagno).

https://doi.org/10.1016/j.cortex.2019.04.009

for this function. In a perspective of saving cognitive resources, such mechanism would be ideally transmodal, supporting the retention of serial order for any kind of information, regardless of its specific content (e.g., verbal, spatial, motor, sensory).

So far, there is no definitive evidence of the existence of such system for the short-term retention of serial order, nor its neural bases have been definitely identified (e.g., Gorin, Mengal, & Majerus, 2018; Hurlstone, Hitch, & Baddeley, 2014). A different type of order memory, namely long-term maintenance of the temporal order of events and experiences in episodic memory, has been extensively studied and a role for the hippocampus has been suggested (see: Davachi & DuBrow, 2015).

On the contrary, the present study aims at investigating whether there is a brain structure involved in retaining serial order in short-term memory (STM), independently from the nature of the stimulus (auditory-verbal, visuo-spatial, motor). For the sake of clarity, STM refers to the temporary storage of a limited amount of information and, critically, does not involve manipulation of such information, which, in contrast, is the distinguishing feature of working memory (see for example Papagno & Cecchetto, 2019; Salis, Martin, Meehan, & McCaffery, 2018).

Specific neural correlates have been found for the components of the subsystem responsible for auditory-verbal STM in the Baddeley and Hitch's working memory model (1974). Evidence comes from anatomo-clinical studies in brain-damaged patients (see Shallice & Papagno, 2019 for a review), neuroimaging studies with positron emission tomography (Awh, Smith, & Jonides, 1995; Poeppel, 1996) and functional magnetic resonance imaging (fMRI) (Henson, Burgess, & Frith, 2000; Paulesu, Frith, & Frackowiak, 1993), and repetitive transcranial magnetic stimulation (rTMS) experiments (Romero Lauro, Walsh, & Papagno, 2006). Such different methodologies converge in supporting the hypothesis that the short-term storage of verbal material and the rehearsal process depend on the activity of two discrete regions in the left hemisphere: the inferior parietal lobule [more specifically, the supramarginal gyrus (SMG), Brodmann's area (BA) 40, but also the angular gyrus, BA 39, see for example Newhart et al., 2012; Vallar, DiBetta, & Silveri, 1997; Warrington, Logue, & Pratt, 1971] and the inferior frontal operculum (BA 44 and BA 6, but also BA 45), respectively.

The working memory model proposed by Baddeley and Hitch suggests the existence of different buffers storing different types of material, i.e., visuo-spatial or verbal, but it does not make any specific assumption concerning the distinction between the identity of the item to be remembered and its serial order (Baddeley & Hitch, 1974).

Evidence from experimental psychology shows that the two types of information, order and item, are stored separately, as first suggested by Bjork and Healy (1974). For example, phonological similarity improves item recall, but it increases order errors (Hulme et al., 1997; Saint-Aubin & Poirier, 1999). Moreover, item recall is more affected by linguistic knowledge than order recall (see for example Saint-Aubin & Poirier, 2000; but see Ward, Avons, & Melling, 2005 for a different position). Recent work also suggests that serial order information can be processed using different codes such as item-to-item association, or start-anchored or end-anchored position (e.g., Fischer-Baum & McCloskey, 2015), as well as depending on their rhythm in spoken sequences (Hartley, Hurlstone, & Hitch, 2016). Finally, recall of temporal order information is more accurate with congruent spatial order information (Fischer-Baum & Benjamin, 2014).

So far, the existence of a specific neural substrate for order retention in STM is still an open issue. Human studies point to a key role of the left SMG/angular gyrus at least for verbal material, as recently confirmed in an fMRI study (Yue, Martin, Hamilton, & Rose, 2018). Moreover, interfering with the activity of this area disrupts the order of short-term auditory-verbal items, rather than affecting item recall, while interfering with the left Broca's area (BA 44/45) activity produces the opposite pattern of results (Papagno et al., 2017). Similarly, an increasing number of neuropsychological studies has indicated that brain damage can impair separately item or order information (for a review see Majerus, 2019). Further support to the existence of a neural representation of order in the left SMG (and in general in the left inferior parietal lobule, of which the SMG is the anterior portion) comes from fMRI studies (e.g., Attout, Fias, Salmon, & Majerus, 2014; Fias, Lammertyn, Caessens, & Orban, 2007; Kalm & Norris, 2014, 2017), although neuroimaging evidence is controversial (Majerus et al., 2006, 2010). Nonetheless, the current literature supports the coding of serial order information in the left SMG for auditory-verbal information, but limited evidence is available for different material, as for visual sequences.

Recently, it has been demonstrated that common behavioral mechanisms and principles contribute to the representation of serial order across the verbal, visual, and spatial STM domains (Hurlstone & Hitch, 2018), possibly with the contribution of the episodic buffer. In a different perspective, some authors (Cowan, Li, Muffin et al., 2011) have suggested the existence of an abstract working memory system (and not simply a common substrate for serial order representation), with the left intraparietal sulcus as its neural correlate.

Here, we propose that the left SMG may act as a general store for serial order computation. To verify this hypothesis, hence to assess how sequential information is stored in STM, we modulated, in healthy participants, the activity of the left SMG, and of the left inferior frontal gyrus (IFG, BA 44) as a control area, by means of low frequency (1 Hz) rTMS. TMS is a non-invasive brain stimulation techniques which allows to prove, on healthy subjects, the causal relationship between a stimulated area (i.e., SMG) and its involvement in a cognitive function (Bolognini & Ro, 2010). In three different experiments, participants' ability to retain serial order in a specific domain was tested, asking them to perform an auditory-verbal (digit span, *Experiment* 1), visuo-spatial (computerized Corsi span, *Experiment* 2) and motor (finger tapping span, *Experiment* 3) STM task. In a fourth experiment (*Control experiment*), we assessed SMG selectivity for order processing using a visual pattern span that does not require the retention of serial information. We focused on the left SMG and left IFG (namely, Broca's area), because our starting point was the Baddeley and Hitch's model; according to this model, auditory-verbal STM includes a buffer, whose neural correlate is the left SMG (see Papagno, 2018 for a review), and a process of rehearsal, with Broca's area and the premotor cortex as neural correlates. In addition, since in a previous study (Papagno et al., 2017) it was found that direct electrical stimulation over the left SMG disrupts serial order in verbal and non-verbal STM tasks, we reasoned that what is stored in the left SMG might be order information, independently from the type of material. Left IFG/Broca's area would store item information, when stimuli are verbal; accordingly, more item errors were produced with stimulation on this area. Thus, we expected that TMS over the left SMG would increase order errors for all type of material, while stimulation of Broca's area would produce item errors, only if using verbal material (digit span).

We chose to test visuo-spatial span, because it is the most investigated form of STM after auditory-verbal one. We avoid to test tactile memory span, because stimulation over the inferior parietal cortex could spread to the somatosensory areas, impairing tactile abilities and preventing to discriminate whether a consequent decrease in performance could depend from a memory or a sensory impairment. Therefore, to have an additional modality, we assessed motor span. Since we did not aim at assessing working memory, that is manipulation of information stored in STM (see Papagno & Cecchetto, 2019; and Shallice & Papagno, 2019 for reviews), we did not stimulate the dorsolateral prefrontal cortex, which is notably involved in maintenance of temporal working memory information (Roberts, Libby, Inhoff, & Ranganath, 2018); accordingly, we used typical tasks to assess verbal (digit) or visuo-spatial (Corsi) span [see Vallar and Papagno (2002) and Shallice and Cooper (2011)], and we designed a homologue motor span.

## 2. Materials and methods

We report how we determined our sample size, all data exclusions (if any), all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study. Database and the tasks/stimuli used in the present study are publicly archived at https://osf.io/9tgy4/

### 2.1. *Participants*

Seventy-five healthy volunteers took part in the study. In *Experiment 1*, *Experiment 2* and *Experiment 3*, 20 subjects were tested with a within-subject, three-sessions, experimental design (*Experiment 1*: mean age ± standard deviation = 22.4 ± 2.6, mean education = 15 ± 2.2 years, 16 females; *Experiment 2*: mean age = 23.5 ± 4, mean education = 15.4 ± 2.2 years, 15 females; *Experiment 3*: mean age = 22.6 ± 2.5, mean education = 15.2 ± 1.9 years, 11 females). In the *Control experiment*, 15 subjects were tested in a two-sessions within-subject experiment (mean age = 21.6 ± 2.1, mean education = 13.7 ± 1. Years; 11 female). Every subject took part in only one experiment. All subjects were right-handed accordingly to the Edinburgh Inventory (Oldfield, 1971) and none of them had contraindications to TMS accordingly to safety guidelines (Rossi, Hallett, Rossini, & Pascual-Leone, 2011). All subjects were naive to the purpose of the study and participated in only one experiment. Before taking part in the study, they gave written informed consent. The study took place in the TMS laboratory of the Department of Psychology of the University of Milano-Bicocca. The protocol was performed in accordance with the ethical standards of the Declaration of Helsinki and was approved by the Ethical Committee of the University of Milano-Bicocca. No part of the study procedures was pre-registered prior to the research being conducted. The sample size was determined by means of an *a-priori* RM-ANOVA within subjects (effect size F = .4; Alpha Error Level: $p$ = .01; Statistical Power = .80, Actual Power = .81).

### 2.2. *Auditory-verbal digit span task (Experiment 1)*

In *Experiment 1*, a computerized auditory-verbal digit span task was administered (Fig. 1a). Subjects sat comfortably in a slightly lit room. The experimenter sat in front of them facing the PC-monitor on the table. The PC-keyboard was hidden under the table so that subjects could not see it during task execution. Subjects were auditory presented with forty-five different sequences, whose length was set at their span, in a randomized order. Spoken digits (1–9) were digitally recorded (file length: 1000 ms) and were delivered through two speakers at the rate of one every 1500 ms. Immediately after presentation, the subject had to recall it. The experimenter reported the given verbal responses using the PC-keyboard. Omitted digits were signed as “misses” in the output of the response by pressing the “0”. Once the sequence was scored, a delay of 1000 ms preceded the presentation of the following sequence. The task lasted approximately 10 min.

### 2.3. *Computerized Corsi visuo-spatial span (Experiment 2)*

A computerized version of the Corsi block-tapping task (Corsi, 1972, pp. 14–69) was administered in *Experiment 2* (Fig. 1b). Subjects sat in front of the PC-monitor in a slightly lit room. Forty-five different sequences, at the subjects' individual span, were visually presented in a randomized order. Each trial started with a fixation cross in the center of the screen for 1000 ms. Then, nine blue squares appeared in nine fixed positions according to the ones of the standard Corsi test. In order to present the sequence, a given number of squares, depending on the sequence length, lit up for 750 ms with an ISI of 750 ms from each other. Once the presentation of the sequence was over, a grey mask appeared for 500 ms and then nine white squares reappeared on the screen. Subjects had to reproduce the sequence by clicking with the PC-mouse over the squares. Every time the subject selected a square (whether it was correct or wrong), an auditory feedback was given. In addition to the nine squares, a “*Don't remember*” button was displayed on the left corner of the screen: the participant could press it to report a missed position. Once the sequence was reproduced, the subject pressed a button to see the following sequence. The task length was of approximately 10 min.

### 2.4. *Finger tapping span task (Experiment 3)*

In *Experiment 3*, a computerized finger tapping span was administered (Fig. 1c). The subject sat in front of the PC-monitor and the PC-keyboard (QWERTY) in a slightly lit

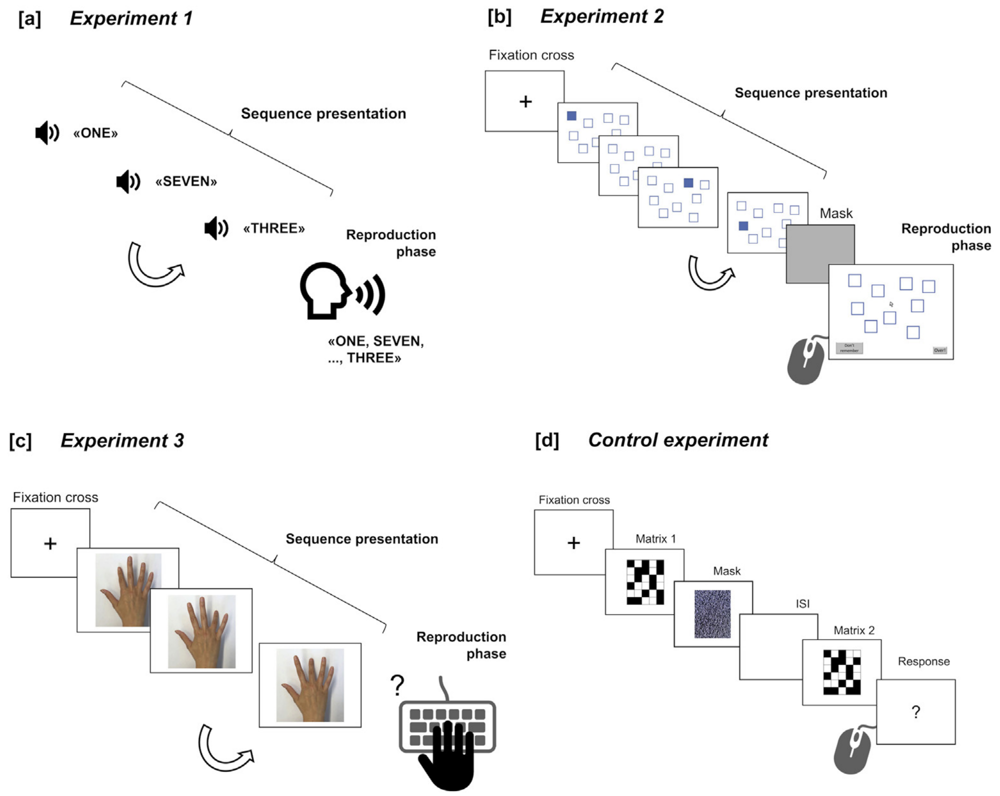

**Fig. 1 – Experimental tasks. [a] Auditory-verbal digit span task. [b] Computerized Corsi span task. [c] Finger tapping motor span task. [d] Visual pattern span task. The number of stimuli, in *Experiment* 1, 2 and 3 and the grid dimension of the matrices, in the *Control experiments*, were based on each subject's span.**

room. Forty-five different finger-tapping sequences, at the subject's individual span length were visually presented in a randomized order. Each trial started with a fixation cross in the center of the screen for 1000 ms. Then, according to the subject's motor span, a sequence of video clips of finger tapping movements was presented. Finger tapping videos depicted a movement made with one of four different fingers of the right hand (thumb tapping movements were excluded due to the discomfort in pressing the keyboard with the thumb while maintaining a natural position of the hand). The clip of each single finger movement lasted 1000 ms and the four clips were filmed to create a natural movement when presented, in a randomized order, one after the other. The hand movements were seen from an egocentric view on a white background. After the sequence presentation, a question mark appeared on the screen and the subject had to press, on the keyboard, the appropriate keys to recreate the sequence. Selected keys were "*d*" for the index finger, "*t*" for the medium finger, "*u*" for the ring finger and "*l*" for the little finger. These keys were chosen so that the subject could hold his hand on the keyboard in the same position as the one seen on the monitor. An additional key, "*z*", had to be pressed, with the index finger of the left hand, for a missed movement. Every time a key (whether correct or wrong) was pressed an auditory feedback was provided. Participants were instructed to keep their eyes fixating the screen during the reproduction phase. On average, the task length was of approximately 10 min.

### 2.5. *Visual pattern span task (Control experiment)*

A computerized visual pattern span task was administered in the *Control experiment* (Fig. 1d), similar to the one adopted in previous TMS studies (Romero Lauro et al., 2006; Romero Lauro, Reis, Cohen, Cecchetto, & Papagno, 2010). This could be considered an easier task compared to the previous ones, but global accuracy in this control test did not differ from global accuracy in the three experimental tasks (see p. 14). The subject sat in a slightly lit room in front of the PC-screen and the keyboard. Forty-eight randomized pairs of checkerboards (24 equal, 24 differing in one square; all with half of the squares on the grid black and half white) were presented. Each trial started with a fixation cross (duration: 2000 ms) followed by the first checkerboard (250 ms). After this, a grey mask briefly appeared (200 ms) followed by a blank screen (1300 ms). Then, the second checkerboard appeared (250 ms). As soon as the second checkerboard disappeared, subjects had to press, on the PC-keyboard, key "1" if the two checkerboards were identical or key "2" if they were different. The participant had 2000 ms to answer before the next trial automatically started and their response was considered omitted. The task lasted about 5 min.

### 2.6. *Individual span assessment*

At the beginning of the first session, each subject performed a modified version of the experimental task (described in the previous paragraphs) to assess their individual span (i.e.,: the length of the sequences to use in *Experiment* 1, 2 and 3, the dimension of the checkerboards for the *Control experiment*). Specifically, blocks of 10 sequences/pairs of checkerboards of increasing difficulty (starting from 5-stimuli sequences and 3 × 4 grids to 9-stimuli sequences and 7 × 4 grids) were presented to the subjects. The individual span was set as the length of the sequences presented in the last block with accuracy >60%. If in this block accuracy was 100%, the sequence length to use in the experiment was increased of one item, even if at this length accuracy was worse than 60%, to prevent ceiling effects during the experimental task. On average, in *Experiment* 1, auditory-verbal span of the subjects was 6.5 ± .8. In *Experiment* 2, visuo-spatial span was 6.3 ± .5. In *Experiment* 3, motor span was: 5.5 ± .5, in the *Control experiment*, the dimension of the grid was 6 × 5.

For all tasks, trials randomization, timing of the stimuli and recording of the subjects' responses were under computer control (E-Prime 3.0, Psychology Software Tool, Inc., www.psychtoolbox.org).

### 2.7. *Repetitive transcranial magnetic stimulation (rTMS)*

An offline, low-frequency (1 Hz) repetitive TMS (rTMS) protocol was used in the four experiments. This protocol was proved to be effective in inhibit the activity of both IFG and SMG (Deschamps, Baum, & Gracco, 2014; Romero Lauro et al., 2010). 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 10 min (for a total of 600 pulses) and intensity was set at 100% of the subject's resting Motor Threshold (rMT). rMT was calculated in each session as the minimum stimulator output able to elicit a detectable motor twitch in the contralateral (right) hand 5 times out of 10 while the left motor cortex was stimulated (Rossi, Hallett, Rossini, & Pascual-Leone, 2009). In *Experiment 1,* the mean rMT was 56.1% ± 4.8% for the IFG session, and 56.3 ± 5.0% for the SMG session; in *Experiment* 2 it was 55.3 ± 5.8% for the IFG session, and 55.9% ± 5.8% for the SMG session; in *Experiment 3,* 54.4 ± 5.3% for the IFG session and 55.3 ± 5.7% for the SMG session; in the *Control experiment* it was 54.3 ± 6.8%. Within a single experiment, the rMTs in the two experimental sessions were not significantly different one from the other ($p > .5$). We localized the targeted areas (Fig. 2a) in each subject and in each rTMS session, using the SoftAxic 2.0 neuronavigation software (E.M.S., Bologna, Italy, www.softaxic.com). This system allows for the reconstruction of the brain in Talairach coordinates (Talairach & Tournoux, 1988) on the basis of digitised skull landmarks (nasion, inion, and two pre-auricular points) as well as 60 uniformly distributed points that are mapped on the scalp via a graphic user interface and a 3D optical digitizer (NDI, Polaris Vicra). An estimation of the single subject's cerebral volume is automatically calculated by means of a warping procedure, through the use of a generic MRI volume on the basis of the set of points previously digitized from the subject's scalp. The mean Talairach coordinates of left IFG (X = −46, Y = 2, Z = 16) and left SMG (X = −44, Y = −32, Z = 24) were taken from previous rTMS studies (Romero Lauro et al., 2010, 2006), and were adapted from previous fMRI peak activations found in verbal STM tasks (Paulesu et al., 1993). During IFG and SMG stimulation, the coil was applied tangentially on the subject's scalp with the handle pointing posteriorly parallel to the subject's midsagittal plane, thus inducing a posterior to anterior current flow.

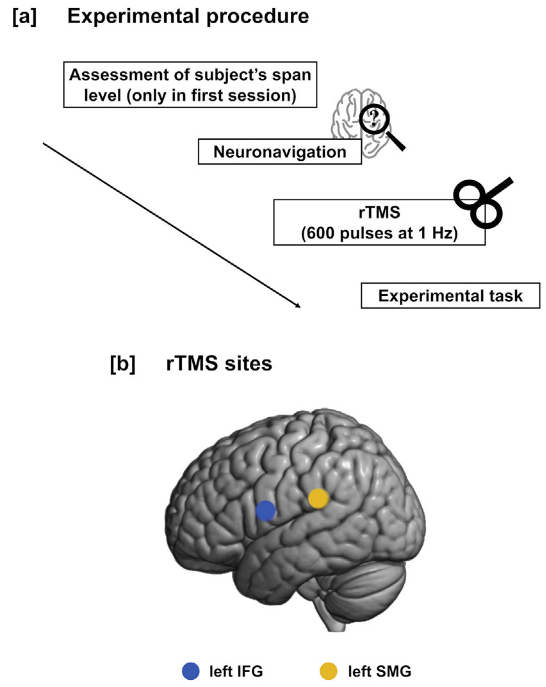

**Fig. 2 – Experimental design. [a] Experimental procedure of the rTMS sessions. In the baseline, subjects underwent the experimental task without rTMS. [b] Lateral view of a 3-D brain reconstruction showing the localization of the rTMS sites. On average, the location of these points was centered on Talairach coordinates X = −44, Y = −32, Z = 24 (left SMG) and X = −46, Y = 2, Z = 16 (left IFG).**

### 2.8. *Experimental procedure*

The experimental procedure and setting were the same in all the experiments (Fig. 2b). During the first session, after obtaining the informed consent and administering the Edinburgh Inventory and the TMS safety checklist questionnaire, we assessed the subject's span. In *Experiments* 1, 2 and 3, participants were invited to report every digit/square/finger movement in the same order of presentation (or what they thought to be the exact order of presentation), or, if a specific item was not remembered, to report that the information was missing. In *Experiment* 3, at the end of the last session, a brief questionnaire was administered to the subjects investigating which kind of retention strategy was used during the motor task; the questionnaire comprised the following 2 items: Q1 - "Did you use any mnemonic strategy during the experimental task?"; Q2 - "If you used any strategy, please describe it". Nine subjects reported to use a mnemonic strategy but none of them described the use of a verbal or visuo-spatial one.

In the Baseline session, no rTMS was delivered. This session was the shortest one and lasted approximately 20 min. In the rTMS sessions, neuronavigation procedures were carried out, then the subject's rMT was assessed, and, finally, rTMS was delivered according to the stimulation site (IFG or SMG). The experimental task was performed immediately after the rTMS protocol. rTMS sessions lasted approximately 75 min. Sessions order was counter-balanced across subjects. In all four experiments, an interval of at least 24 h divided the two sessions.

### 2.9. *Error scoring (Experiments 1, 2, 3)*

Errors were scored using the St. Aubin and Poirier's method (Saint-Aubin & Poirier, 1999), as done in previous studies on brain-damaged patients (Papagno et al., 2017; Papagno, Vernice, & Cecchetto, 2013). This scoring method has been previously adopted for auditory-verbal span, but not for visuo-spatial and motor span. Our three experimental tasks were specifically built to provide the same type of response output in order to analyze the data with the same method for each span task.

Item errors included: *i) substitution,* i.e., when an item was replaced with a different not present in the original sequence (e.g., 1234 → 1274); *ii) omission,* i.e., when an item was not produced at all (e.g., 1234 → 123). Conversely, order errors included: *i) inversion,* i.e., when two items were reported at each other's serial position (e.g., 1234 → 1324)*; ii) permutation*, i.e., when an item was reported at the wrong serial position without disturbing the order of the remaining items (e.g., 1234 → 2341). According to St. Aubin & Poirier's scoring method, when an *inversion* was made it was scored as 2 order errors, while *permutations* were scored as 1 order error (in order to avoid overestimation) (Saint-Aubin & Poirier, 1999). Whenever more than one order error was made, a conservative scoring approach was adopted to compute this kind of errors: for instance, a recalled sequence "1754", when the presented one was "4517", was scored having 2 *permutations* errors ("4" after the "1–7" chunk and "5" between the "4" and the "1–7" chunk). Furthermore, if both kinds of error were present in a sequence, for the computation of order errors, the serial position of item errors was considered: for instance, the sequence "1234", recalled as "2153", was scored as including 1 *substitution* and 2 *inversion* errors, considering the correct serial position of the wrong item "5" as the one of the originally presented "4". Then, the proportion of item and order errors for each sequence was computed. To account for the increasing probability of producing order errors with longer sequences, the number of order errors in a sequence was divided by the total number of recalled items within the same sequence (Papagno et al., 2017; Saint-Aubin & Poirier, 1999). Every output was scored independently by two different experimenters, who were blind to the experimental condition.

### 2.10. *Statistical analysis*

The Kolmogorov–Smirnov test confirmed the normality of the distributions for all the experiments, and when appropriate, data sphericity was confirmed by Mauchly's test. Statistical significance was set with $p \leq .05$. None of the tested subjects was excluded from the sample due to outlier values (set at ± 2 standard deviations).

First, a one-way between-subjects analysis of variance (ANOVA) was conducted to compare the subjects' accuracy in the Baseline session of the four experiments to assess whether their difficulty was comparable.

For the digit span, the Corsi span and the finger tapping span, the proportions of item and order errors produced within the sequences of the experimental tasks were analyzed using 3 × 2 repeated-measures ANOVA (rm-ANOVA), with the within-subjects factors "Stimulation" (3 levels: "Baseline", "IFG rTMS", "SMG rTMS") and "Type of error" (2 levels: "proportion of item errors", "proportion of order errors").

Finally, the proportions of item and order errors produced in the three main experiments were also directly compared with a rm-ANOVA with the between-subjects factor "Experiment" and the within-subjects factors "Stimulation" and "Type of error" (both these factors have the same levels of the previous analysis).

In the control experiment, we considered subjects' accuracy in the visual pattern span task and proportion of errors made in the trials where the pairs of matrices were different. Dependent samples *t*-tests were conducted to compare these variables in the baseline and SMG stimulation condition.

Post-hoc analyses were corrected by applying Bonferroni correction for multiple comparisons. All analyses were conducted using Statistica software (v. 10, StatSoft).

## 3. Results

The preliminary ANOVA run to compare the subjects' accuracy in the Baseline condition of the four experimental tasks showed no significant difference ($F_{(3,\ 71)} = .672$, $p = .572$, $\eta p^2 = .03$), hence confirming a comparable level of difficulty between tasks (all results are reported as mean ± standard error – SE; $\text{accuracy}_{\text{digit span}} = 73.9 \pm 2.5\%$, $\text{accuracy}_{\text{Corsi span}} = 69.6 \pm 3.5\%$, $\text{accuracy}_{\text{motor span}} = 69.3 \pm 2.9\%$, $\text{accuracy}_{\text{visual pattern span}} = 73.3 \pm 2.6\%$).

### 3.1. *Experiment 1*

Regarding error types in the auditory-verbal digit span, a significant "Stimulation" by "Type of error" interaction emerged from rm-ANOVA ($F_{(2,38)} = 15.586$, $p < .001$, $\eta p^2 = .45$). Subjects produced more item errors after stimulation of IFG (5.4 ± .7%) than after stimulation of SMG (3.8 ± .6%; $p = .002$) and baseline session (3.5 ± .5%; $p < .001$). Item errors occurring in the baseline condition and after rTMS over SMG did not differ significantly ($p = 1$). Conversely, the stimulation of SMG selectively increased order errors (7.5 ± .8%) as compared to IFG (6.0 ± .6%; $p = .01$) and baseline (5.4 ± .6%; $p < .001$) conditions. Crucially, no significant difference was present between rTMS over IFG and baseline condition for order errors ($p = 1$) (Fig. 3 – first column).

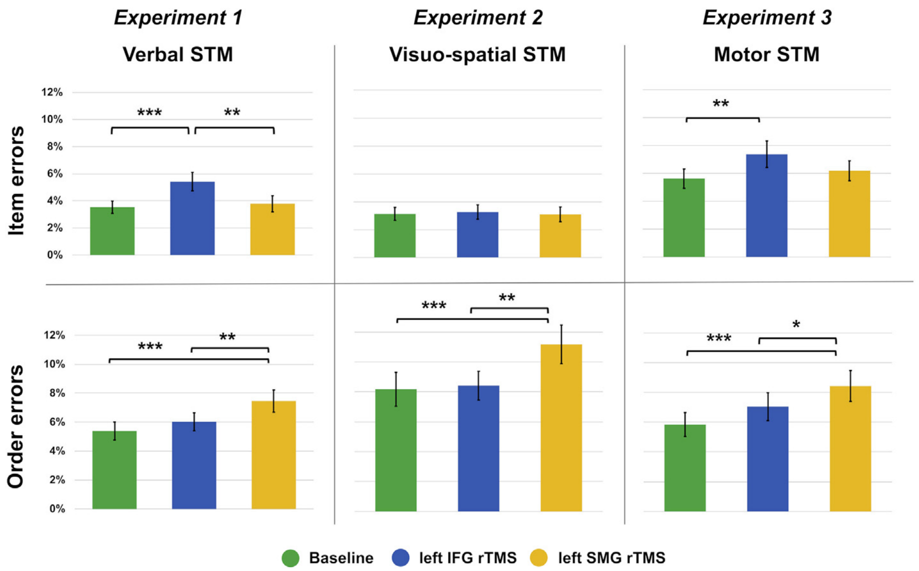

**Fig. 3 – Results of the three main experiments. Proportions of item (upper row) and order errors (lower row) in the three main experiments: digit (1st column), Corsi (2nd column) and motor (3rd column) span tasks. Bonferroni correction for multiple comparisons was applied (legend: *$p < .05$; **$p < .01$; ***$p < .001$). Error bars = SE.**

### 3.2. *Experiment 2*

The rm-ANOVA on the proportion of item and order errors on the computerized Corsi span task revealed a significant "Stimulation" by "Type of error" interaction ($F_{(2,38)} = 6.885$, $p = .003$, $\eta p^2 = .27$). In this second experiment, the three stimulation conditions did not differ concerning the produced item errors (Baseline: 3.1 ± .5%, IFG rTMS = 3.3 ± .5%, SMG rTMS = 3.1 ± .5%; all $p = 1$), while they did for order errors, with SMG stimulation increasing their proportion (11.2 ± 1.3%) compared to the other two sessions (Baseline = 8.2 ± 1.1%, $p < .001$; IFG rTMS = 8.4 ± 1.0%, $p = .002$). Importantly, order errors made in the rTMS IFG and baseline conditions did not differ ($p = .99$) (Fig. 3 – second column).

### 3.3. *Experiment 3*

Also in the finger tapping span task, the rm-ANOVA on the proportion of item and order errors showed a significant "Stimulation" by "Type of error" interaction ($F_{(2,38)} = 10.168$, $p < .001$, $\eta p^2 = .35$). Subjects made more item errors after rTMS over IFG (7.4 ± .9%) than in the baseline condition (5.6 ± .7%; $p = .003$). However, item errors after SMG rTMS (6.2 ± .7%) did not statistically differ from those produced both after IFG rTMS ($p = .124$) and in the baseline condition ($p = .99$). Conversely, order errors significantly increased only after stimulation of SMG (8.4 ± 1.0%; $p_{\text{SMG-Baseline}} < .001$; $p_{\text{SMG-IFG}} = .034$), while there were no differences between IFG rTMS (7.0 ± .9%) and baseline condition (5.8 ± .8%; $p = .113$) (Fig. 3 – third column).

### 3.4. *Comparisons of the three main experiments results*

When comparing the proportion of item and order errors produced in the three span tasks, we found a significant "Stimulation" by "Type of error" interaction ($F_{(2,114)} = 26.947$, $p < .001$, $\eta p^2 = .32$), which confirmed the previous findings, namely: regardless of the experiment, post-hoc comparisons showed that order errors increases only after SMG rTMS (9 ± .6%, $p < .001$), as compared to the baseline (6.5 ± .5%) and IFG rTMS (7.2 ± .5%); conversely, item errors increased only after IFG stimulation (5.4 ± .5%, $p < .006$), as compared to the baseline (4.1 ± .3%). Importantly, the "Experiment" by "Stimulation" by "Type of error" interaction did not reach significance ($F_{(2,114)} = .62$, $p = .65$, $\eta p^2 = .02$).

### 3.5. *Control experiment*

In the *Control experiment*, no significant differences occurred between baseline (accuracy: 73.3 ± 2.6%; proportion of errors: 36.4 ± 2.6%) and SMG rTMS (accuracy: 73.1 ± 2.8%; proportion of errors: 35.5 ± 2.2%) for both accuracy ($t_{(14)} = .093$, $p = .927$) and proportion of errors made in "different matrices" trials ($t_{(14)} = .36$, $p = .725$) (Fig. 4).

## 4. Discussion

In the present study, for the first time, we demonstrate that order retention in STM is independent from the nature of the presented material, finally clarifying the cognitive and neural mechanisms underlying this process. We found that suppression of the left SMG activity disrupted serial order retention in verbal, visuo-spatial and motor span tasks, while no effect was found on item errors. Results in a STM task not involving order retention confirmed the specificity of our findings. By contrast, a selective modulation of item errors was found only after stimulation of the left IFG, both in the verbal and motor span tasks. In fact, a previous behavioural study on healthy participants (Johnson, Shaw, & Miles, 2016)

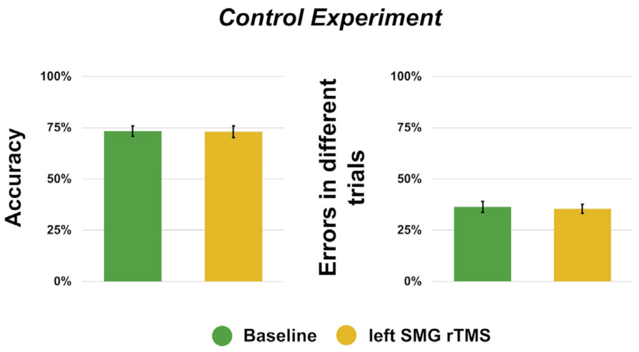

**Fig. 4 – Results of the Control experiment. Left panel: accuracy; right panel: proportion of errors in trials with two different matrices.**

demonstrated, for tactile order memory, the same serial position effects and error distribution found with visual or verbal stimuli. However, this study does not offer any anatomical information and does not directly compare the same task (which was not a typical span task) using different types of material as we did.

Serial order is maintained through associations of each item with an independent representation of the position that the item holds in the sequence (Ginsburg, Archambeau, van Dijck, Chetail, & Gevers, 2017). So far, there has been an important debate about domain-specific or domain-general processing of serial order in STM. On the one hand, recent studies support the idea that serial order coding involves domain-specific mechanisms (Saito, Logie, Morita, & Law, 2008; Soemer & Saito, 2016). For example, Soemer and Saito (2016) making use of dual-task paradigms showed an interference for serial order performance within modalities but a weak interference between modalities. On the other hand, the existence of a unitary model of serial order coding in STM, in which all items (verbal, spatial or visual) share a common representation (for a review see Hurlstone et al., 2014), has been put forward but never demonstrated. The present results provide empirical support to this view, in line with recent observation in neurosurgical patients with direct electrical stimulation of the left SMG eliciting order errors in meaningless shapes span (Papagno et al., 2017). A further support comes from a TMS study assessing the role of the SMG in phonological processing that demonstrated the involvement of SMG in memory tasks but not in phonology (Deschamps et al., 2014).

Similarly, Kalm and Norris (2014) used fMRI and a serial recall task to dissociate neural activity patterns representing the phonological properties of the items stored in STM from the patterns representing their order. They show that a set of brain areas in the postero-dorsal stream of auditory processing store associations between items and order as predicted by a positional model. Therefore, their results favor a neural model of order representation that stores item codes, position codes, and the mapping between them. We extend this result, suggesting that position codes are stored in the same region, independently from the nature of items. In this sense, we are not arguing that these codes are operated by the central executive, but that some part of the brain is sensitive to serial position not as a stored feature of stimuli, but as computational processes, the output of which is the item in the appropriate position.

In the same vein, Hurlstone and Hitch (2018) suggested that common mechanisms and principles contribute to the representation of serial order across the verbal, visual, and spatial STM domains. Burgess and Hitch (2005) postulated that this locus might be the episodic buffer and that the buffer might serve as a common positional coding mechanism for items maintained in the phonological loop and the visuospatial sketchpad.

A challenge for the future will be to clarify what makes the difference across the verbal, visual, and spatial domains, since it is well-known that verbal and spatial STM impairments dissociate in neuropsychological patients [Shallice and Papagno (2019) for a review].

The results found on item errors after the stimulation of left IFG are in line with the previous literature on the role of this cortical area. Regarding verbal STM, it is well-known that the left IFG a core region of the phonological loop (e.g., Baddeley & Hitch, 2019; Papagno et al., 2017; Paulesu et al., 1993; Romero et al., 2006). Instead, with respect to motor STM, the increase of item errors after IFG stimulation may be linked to an impairment of the action observation network (Rizzolatti & Craighero, 2004). Indeed, IFG is considered a core region of this network (Caspers, Zilles, Laird, & Eickhoff, 2010; Molnar-Szakacs, Iacoboni, Koski, & Mazziotta, 2005); accordingly, Hamzei et al. (2016) found that IFG is strongly activated during tasks for which action observation is related to imitation, as in our motor span. We suggest that its inhibition by means of rTMS impaired processing of observed movements, leading to a loss of content information when these movements had to be reproduced.

As Lashley already wrote in 1951 "*Certainly language presents in a most striking form the integrative functions that are characteristic of the cerebral cortex and that reach their highest development in human thought processes. Temporal integration is not found exclusively in language; the coordination of leg movements in insects, the song of birds, the control of trotting and pacing in a gaited horse, the rat running the maze, the architect designing a house, and the carpenter sawing a board present a problem of sequences of action …*" (Lashley, 1951, pp. 112–147). We tried to contribute to this issue, providing experimental evidence that a single network is responsible for the maintenance of serial order (namely, temporal integration) in all domains. In this network the left SMG is a crucial (even if not the only) node together with other regions, such as the ventral frontal and opercular cortex (Wilson, Marslen-Wilson, & Petkov, 2017).

Of course, we are aware that rTMS produces diffuse results and can affect both stimulated and non-stimulated brain regions (Abe, Fukuyama, & Mima, 2014). Therefore, the observed results are not necessarily due to the direct effect of stimulation on a specific region, but they can as well reflect the changes in connectivity among multiple regions. This is the main limitation of our study, and generally speaking, of all rTMS studies. However, the present results add to a consistent amount of converging data from the literature on brain-damaged patients in suggesting a role for the left SMG gyrus in STM. Similarly, the contribution of right hemisphere regions cannot be excluded, since we assessed only left-brain sites. Moreover, we acknowledge that our control task, consisting in a comparison-based visual pattern task, although similar in terms of overall level of difficulty (same level of response accuracy[1]), could differ from the main tasks with respect to the involved cognitive processes, which likely recruit other cortical areas besides SMG.

Finally, our results are not in contrast with the Baddeley and Hitch's working memory model; we suggest the existence of a buffer that computes order information, while the item storage occurs in a specific, unimodal buffer, which in the case of verbal material corresponds to left IFG/Broca's area. Accordingly, we disagree with models suggesting an abstract working memory (Cowan et al., 2011), since there is clear evidence from studies on brain-damage patients that verbal and visuo-spatial STM dissociate (Shallice & Papagno, 2019, for a review). Yet, we assume that information concerning serial order could be stored, separately, in the left SMG. Further research should investigate the possibility for left brain-damaged patients to show an increase of order errors in their spatial span compared to matched controls. Since visuo-spatial span is usually in the normal range in these patients, further TMS research should explore the role of the right SMG.

## Declarations of interest

None.

## Funding

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

## Open practices

The study in this article earned Open Materials and Open Data badges for transparent practices. Materials and data for the study are available at https://osf.io/9tgy4/.

## CRediT authorship contribution statement

**Giacomo Guidali:** Data curation, Formal analysis, Investigation, Writing - review & editing. **Alberto Pisoni:** Data curation, Investigation, Writing - review & editing. **Nadia Bolognini:** Methodology, Supervision, Writing - review & editing. **Costanza Papagno:** Conceptualization, Methodology, Project administration, Writing - original draft, Writing - review & editing.

## Acknowledgments

We would like to thank Alessia Nicotra and Camilla Roncoroni for their valuable help in data collection and Carlo Toneatto for his helpful technical assistance.

## REFERENCES

Abe, M., Fukuyama, H., & Mima, T. (2014). Water diffusion reveals networks that modulate multiregional morphological plasticity after repetitive brain stimulation. *Proceedings of the National Academy of Sciences, 111*(12), 4608–4613. https://doi.org/10.1073/pnas.1320223111.

Attout, L., Fias, W., Salmon, E., & Majerus, S. (2014). Common neural substrates for ordinal representation in short-term memory, numerical and alphabetical cognition. *PLos One, 9*(3). http://doi.org/10.1371/journal.pone.0092049.

Awh, E., Smith, E. E., & Jonides, A. N. D. J. (1995). Human rehearsal processes and the frontal Lobes: PET evidence. *Annals of the New York Academy of Sciences*, 97–117.

Baddeley, A. (2012). Working memory: Theories, models, and controversies. *Annual Review of Psychology, 63*(1), 1–29. http://doi.org/10.1146/annurev-psych-120710-100422.

Baddeley, A. D., & Hitch, G. J. (1974). Working memory. In *Psychology of learning and motivation* (pp. 47–89). Academic Press.

Baddeley, A. D., & Hitch, G. J. (2019). The phonological loop as a buffer store: An update. *Cortex, 112*, 91–106. http://doi.org/10.1016/j.cortex.2018.05.015.

Bjork, E. L., & Healy, A. F. (1974). Short-term order and item retention. *Journal of Verbal Learning and Verbal Behavior, 13*(1), 80–97. http://doi.org/10.1016/S0022-5371(74)80033-2.

Bolognini, N., & Ro, T. (2010). Transcranial magnetic stimulation: Disrupting neural activity to alter and assess brain function. *Journal of Neuroscience, 30*(29), 9647–9650. http://doi.org/10.1523/JNEUROSCI.1990-10.2010.

Burgess, N., & Hitch, G. (2005). Computational models of working memory: Putting long-term memory into context. *Trends in Cognitive Sciences, 9*(11), 535–541. http://doi.org/10.1016/j.tics.2005.09.011.

Caspers, S., Zilles, K., Laird, A. R., & Eickhoff, S. B. (2010). ALE meta-analysis of action observation and imitation in the human brain. *Neuroimage, 50*(3), 1148–1167. http://doi.org/10.1016/j.neuroimage.2009.12.112.

Corsi, P. (1972). *Human memory and the medial temporal lobe region of the brain*. Montreal: McGill University.

Cowan, N., Li, D., Moffitt, A., Becker, T. M., Martin, E. A., Scott Saults, J., et al. (2011). A neural region of abstract working memory. *Journal of Cognitive Neuroscience, 23*(10), 2852–2863. http://doi.org/10.1162/jocn.2011.21625.

Davachi, L., & DuBrow, S. (2015). How the hippocampus preserves order: The role of prediction and context. *Trends in Cognitive Sciences, 19*(2), 92–99. http://doi.org/10.1016/j.tics.2014.12.004.

Deschamps, I., Baum, S. R., & Gracco, V. L. (2014). On the role of the supramarginal gyrus in phonological processing and verbal working memory: Evidence from rTMS studies. *Neuropsychologia, 53*, 39–46. http://doi.org/10.1016/j.neuropsychologia.2013.10.015.

Fias, W., Lammertyn, J., Caessens, B., & Orban, G. A. (2007). Processing of abstract ordinal knowledge in the horizontal segment of the intraparietal sulcus. *Journal of Neuroscience, 27*(33), 8952–8956. http://doi.org/10.1523/JNEUROSCI.2076-07.2007.

Fischer-Baum, S., & Benjamin, A. S. (2014). Time, space, and memory for order. *Psychonomic Bulletin & Review, 21*(5), 1263–1271. http://doi.org/10.3758/s13423-014-0604-7.

---

[1] The control task is based on a comparison process, not on a reproduction one as the main tasks; however, by comparing the performance of 15 healthy adults (mean age = 24.7 years) at the ‘comparison’ version of the visual pattern span task and at a ‘reproduction’ version of the same task, we did not found any difference in the level of accuracy (73% ± 2.4% *vs* 72% ± 4%, $t_{14} = -.23$, $p = .8$), confirming that the two cognitive processes (comparison *vs* reproduction) did not differ at least in term of cognitive load.

Fischer-Baum, S., & McCloskey, M. (2015). Representation of item position in immediate serial recall: Evidence from intrusion errors. *Journal of Experimental Psychology. Learning, Memory, and Cognition, 41*(5), 1426–1446. http://doi.org/10.1037/xlm0000102.

Ginsburg, V., Archambeau, K., van Dijck, J. P., Chetail, F., & Gevers, W. (2017). Coding of serial order in verbal, visual and spatial working memory. *Journal of Experimental Psychology: General, 146*(5), 632–650. http://doi.org/10.1037/xge0000278.

Gorin, S., Mengal, P., & Majerus, S. (2018). A comparison of serial order short-term memory effects across verbal and musical domains. *Memory & Cognition, 46*(3), 464–481. http://doi.org/10.3758/s13421-017-0778-0.

Hamzei, F., Vry, M. S., Saur, D., Glauche, V., Hoeren, M., Mader, I., et al. (2016). The dual-loop model and the human mirror neuron system: An exploratory combined fMRI and DTI study of the inferior frontal gyrus. *Cerebral Cortex, 26*(5), 2215–2224. http://doi.org/10.1093/cercor/bhv066.

Hartley, T., Hurlstone, M. J., & Hitch, G. J. (2016). Effects of rhythm on memory for spoken sequences: A model and tests of its stimulus-driven mechanism. *Cognitive Psychology, 87*, 135–178. http://doi.org/10.1016/j.cogpsych.2016.05.001.

Henson, R. N. A., Burgess, N., & Frith, C. D. (2000). Recoding, storage, rehearsal, and grouping in verbal short-term memory: An fMRI study. *Neuropsychologia, 38*, 426–440. http://doi.org/10.1016/S0028-3932(99)00098-6.

Hulme, C., Roodenrys, S., Brown, G. D. A., Schweickert, R., Martin, S., & Stuart, G. (1997). Word-frequency effects on short-term memory tasks: Evidence for a redintegration process in immediate serial recall. *Journal of Experimental Psychology. Learning, Memory, and Cognition, 23*(5), 1217–1232. http://doi.org/10.1037/0278-7393.23.5.1217.

Hurlstone, M. J., & Hitch, G. J. (2018). How is the serial order of a visual sequence represented? Insights from transposition latencies. *Journal of Experimental Psychology. Learning, Memory, and Cognition, 44*(2), 1–78.

Hurlstone, M. J., Hitch, G. J., & Baddeley, A. D. (2014). Memory for serial order across domains: An overview of the literature and directions for future research. *Psychological Bulletin, 140*(2), 339–373. http://doi.org/10.1037/a0034221.

Johnson, A. J., Shaw, J., & Miles, C. (2016). Tactile order memory: Evidence for sequence learning phenomena found with other stimulus types. *Journal of Cognitive Psychology, 28*(6), 718–725. http://doi.org/10.1080/20445911.2016.1186676.

Kalm, K., & Norris, D. (2014). The representation of order information in auditory-verbal short-term memory. *Journal of Neuroscience, 34*(20), 6879–6886. http://doi.org/10.1523/JNEUROSCI.4104-13.2014.

Kalm, K., & Norris, D. (2017). A shared representation of order between encoding and recognition in visual short-term memory. *Neuroimage, 155*, 138–146. April http://doi.org/10.1016/j.neuroimage.2017.04.047.

Lashley, K. (1951). *The problem of serial order in behavior*. Bobbs-Merril. http://doi.org/10.1093/rfs/hhq153.

Majerus, S. (2019). Verbal working memory and the phonological buffer: The question of serial order. *Cortex*, 122–133. http://doi.org/10.1016/j.cortex.2018.04.016.

Majerus, S., D'Argembeau, A., Perez, T. M., Belayachi, S., Van Der Linden, M., Collette, F., et al. (2010). The commonality of neural networks for verbal and visual short-term memory. *Journal of Cognitive Neuroscience, 22*(11), 2570–2593. http://doi.org/10.1162/jocn.2009.21378.

Majerus, S., Poncelet, M., Van der Linden, M., Albouy, G., Salmon, E., Sterpenich, V., et al. (2006). The left intraparietal sulcus and verbal short-term memory: Focus of attention or serial order? *Neuroimage, 32*(2), 880–891. http://doi.org/10.1016/j.neuroimage.2006.03.048.

Molnar-Szakacs, I., Iacoboni, M., Koski, L., & Mazziotta, J. C. (2005). Functional segregation within pars opercularis of the inferior frontal gyrus: Evidence from fMRI studies of imitation and action observation. *Cerebral Cortex, 15*(7), 986–994. http://doi.org/10.1093/cercor/bhh199.

Newhart, M., Trupe, L. A., Gomez, Y., Cloutman, L., Jarred, J., Davis, C., et al. (2012). Ischemia in Broca's area versus angular gyrus. *Cortex, 48*(10), 1288–1297. http://doi.org/10.1016/j.cortex.2011.09.009.Asyntactic.

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia, 9*(1), 97–113. http://doi.org/10.1016/0028-3932(71)90067-4.

Papagno, C. (2018). Memory deficits. In *Handbook of clinical neurology* (1st ed., Vol. 151). Elsevier B.V http://doi.org/10.1016/B978-0-444-63622-5.00019-X.

Papagno, C., & Cecchetto, C. (2019). Is STM involved in sentence comprehension? *Cortex, 112*, 80–90. http://doi.org/10.1016/j.cortex.2018.08.028.

Papagno, C., Comi, A., Riva, M., Bizzi, A., Vernice, M., Casarotti, A., et al. (2017). Mapping the brain network of the phonological loop. *Human Brain Mapping, 38*(6), 3011–3024. http://doi.org/10.1002/hbm.23569.

Papagno, C., Vernice, M., & Cecchetto, C. (2013). Phonology without semantics? Good enough for verbal short-term memory. Evidence from a patient with semantic dementia. *Cortex, 49*(3), 626–636. http://doi.org/10.1016/j.cortex.2012.04.015.

Paulesu, E., Frith, C. D., & Frackowiak, R. S. J. (1993). The neural correlates of the verbal component of working memory. *Nature, 362*, 342–345.

Poeppel, D. (1996). A critical review of PET studies of phonological processing. *Brain and Language, 55*(3), 317–351. http://doi.org/10.1006/brln.1996.0108.

Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience, 27*(1), 169–192. http://doi.org/10.1146/annurev.neuro.27.070203.144230.

Roberts, B. M., Libby, L. A., Inhoff, M. C., & Ranganath, C. (2018). Brain activity related to working memory for temporal order and object information. *Behavioural Brain Research, 354*, 55–63. June 2017 http://doi.org/10.1016/j.bbr.2017.05.068.

Romero Lauro, L., Reis, J., Cohen, L. G., Cecchetto, C., & Papagno, C. (2010). A case for the involvement of phonological loop in sentence comprehension. *Neuropsychologia, 48*(14), 4003–4011. http://doi.org/10.1016/j.neuropsychologia.2010.10.019.

Romero Lauro, L., Walsh, V., & Papagno, C. (2006). The neural correlates of phonological short-term memory: A repetitive transcranial magnetic stimulation study. *Journal of Cognitive Neuroscience, 18*(7), 1147–1155. http://doi.org/10.1162/jocn.2006.18.7.1147.

Rossi, S., Hallett, M., Rossini, P. M., & Pascual-Leone, A. (2009). Safety, ethical considerations, and application guidelines for the use of transcranial magnetic stimulation in clinical practice and research. *Clinical Neurophysiology, 120*(12), 2008–2039. http://doi.org/10.1016/j.clinph.2009.08.016.

Rossi, S., Hallett, M., Rossini, P. M., & Pascual-Leone, A. (2011). Screening questionnaire before TMS: An update. *Clinical Neurophysiology, 122*(8), 1686. http://doi.org/10.1016/j.clinph.2010.12.037.

Saint-Aubin, J., & Poirier, M. (1999). Semantic similarity and immediate serial recall: Is there a detrimental effect on order information? *The Quarterly Journal of Experimental Psychology Section A, 52*(2), 367–394. http://doi.org/10.1080/713755814.

Saint-Aubin, J., & Poirier, M. (2000). Immediate serial recall of words and nonwords: Tests of the retrieval-based hypothesis. *Psychonomic Bulletin & Review, 7*(2), 332–340. http://doi.org/10.3758/BF03212990.

Saito, S., Logie, R. H., Morita, A., & Law, A. (2008). Visual and phonological similarity effects in verbal immediate serial recall: A test with kanji materials. *Journal of Memory and Language, 59*(1), 1–17. http://doi.org/10.1016/j.jml.2008.01.004.

Salis, C., Martin, N., Meehan, S. V., & McCaffery, K. (2018). Short-term memory in aphasia: Insights from speech-timing measures. *Journal of Neurolinguistics, 48*, 176–189.

Shallice, T., & Cooper, R. P. (2011). *The organization of mind*. Oxford.

Shallice, T., & Papagno, C. (2019). Impairments of auditory-verbal short-term memory: Do selective deficits of the input phonological buffer exist? *Cortex, 112*, 107–121. http://doi.org/10.1016/j.cortex.2018.10.004.

Soemer, A., & Saito, S. (2016). Domain-specific processing in short-term serial order memory. *Journal of Memory and Language, 88*, 1–17. http://doi.org/10.1016/j.jml.2015.12.003.

Talairach, E. E., & Tournoux, P. (1988). *Co-planar stereotactic atlas of human brain: 3-dimensional proportional system: An approach to cerebral imaging*. New York: Stuttgart: Thieme.

Vallar, G., DiBetta, A. M., & Silveri, C. (1997). The phonological short-term storage-rehearsal system: Patterns of impairment and neural correlates. *Neuropsychologia, 35*, 795–812.

Vallar, G., & Papagno, C. (2002). Neuropsychological impairments of short-term memory. In A. D. Baddeley, M. Kopelman, & B. Wilson (Eds.), *Handbook of memory disorders* (pp. 249–270). Chichester: Wiley.

Ward, G., Avons, S. E., & Melling, L. (2005). Serial position curves in short-term memory: Functional equivalence across modalities. *Memory, 13*(3–4), 308–317. http://doi.org/10.1080/09658210344000279.

Warrington, E. K., Logue, V., & Pratt, R. T. C. (1971). The anatomical localisation of selective impairment of auditory verbal short-term memory. *Neuropsychologia, 9*(4), 377–387. http://doi.org/10.1016/0028-3932(71)90002-9.

Wilson, B., Marslen-Wilson, W. D., & Petkov, C. I. (2017). Conserved sequence processing in primate frontal cortex. *Trends in Neurosciences, 40*(2), 72–82. http://doi.org/10.1016/j.tins.2016.11.004.

Yue, Q., Martin, R. C., Hamilton, A. C., & Rose, N. S. (2018). Non-perceptual regions in the left inferior parietal lobe support phonological short-term memory: Evidence for a buffer account? *Cerebral Cortex*, 1–16. http://doi.org/10.1093/cercor/bhy037.