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Research Report

New functional dissociations between prefrontal and parietal cortex during task switching: A combined fMRI and TMS study

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ABSTRACT

Preparatory control in task-switching has been suggested to rely upon a set of distributed regions within a frontoparietal network, with frontal and parietal cortical areas cooperating to implement switch-specific preparation processes. Although recent causal evidence using transcranial magnetic stimulation (TMS) have generally supported this model, alternative results from both functional neuroimaging and neurophysiological studies have questioned the switch-specific role of both frontal and parietal cortices. The aim of the present study was to clarify the involvement of prefrontal and parietal areas in preparatory cognitive control. With this purpose, an fMRI study was conducted to identify the brain areas activated during cue events in a task-switching paradigm, indicating whether to switch or to repeat among numerical tasks. Then, TMS was applied over the specific coordinates previously identified through fMRI, that is, the right inferior frontal gyrus (IFG) and right intraparietal sulcus (IPS). Results revealed that TMS over the right IFG disrupted performance in both switch and repeat trails in terms of delayed responses as compared to Sham condition. In contrast, TMS over the right IPS selectively interfered performance in

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switch trials. These findings support a multi-component model of executive control with the IFG being involved in more general switch-unspecific process such as the episodic retrieval of goals, and the IPS being related to the implementation of switch-specific preparation mechanisms for activating stimulus-response mappings. The results are discussed within the framework of contemporary hierarchical models of prefrontal cortex organization, suggesting that distinct prefrontal areas may carry out coordinated functions in preparatory control.

1. Introduction

Neuroanatomical models about executive control suggest interactions within a frontoparietal network (FPN) of brain regions cooperating for an adjusted and flexible control of human behaviour (Koechlin & Summerfield, 2007; Miller & Cohen, 2001; Petersen & Posner, 2012). General consensus exists among theories assuming that the prefrontal cortex will generate top-down signals to bias processing at posterior areas. Studies using task-switching paradigms in combination with neuroimaging, neurophysiological, and lesional techniques have contributed to clarify the role of different brain regions within this FPN to cognitive control (Kopp et al., 2006; Monchi et al., 2001; Muhle-Karbe et al., 2014; Niendam et al., 2012; Periáñez et al., 2004; Sohn et al., 2000; Worringer et al., 2019). Thus, task-switching requires to change frequently among a set of simple tasks, which is supposed to activate certain control operations that will ultimately allow a flexible adaptive behaviour (Logan & Bundesen, 2003; Monsell, 2003; Wylie & Allport, 2000).

Functional neuroimaging studies have identified switch-specific activation in prefrontal areas such as medial frontal gyrus, inferior frontal gyrus (IFG), and the inferior frontal junction (IFJ), and in parietal areas such as posterior parietal cortex and precuneus, suggesting complementary operations during the implementation of a task switch. For instance, the activation of the IFJ in response to task switch cues has been related to the task preparation processes of updating the task rule or task set that needs to be implemented next (Derrfuss et al., 2005; Kim et al., 2012; Worringer et al., 2019). Within the parietal lobe, the intraparietal sulcus (IPS) has been related to the activation of more concrete task representations such as the mapping of a given stimulus to the response that is adequate according to the currently active task set (Andersen et al., 1997; Culham & Kanwisher, 2001; Worringer et al., 2019). The analysis of the time dynamics of the activation within this FPN by means of neurophysiological techniques have generally supported the idea that activation of prefrontal regions precedes the activation of posterior ones during the implementation of a switch in task (Brass et al., 2005; Kopp et al., 2006; Periáñez et al., 2004; Stuss & Picton, 1978). According to a recent meta-analysis the activation of the FPN seems to be largely bilateral both in anterior and posterior brain areas, with significant convergent clusters across studies in the anterior insula, pre-supplementary motor area, IFJ or IPS, with some left dominant regions in the dorsal-premotor cortex (Worringer et al., 2019). Existing evidence on the possibility of hemispheric specialization patterns among frontoparietal network structures is still limited. For instance, in an early experiment using a computerized version of the Wisconsin Card Sorting Test, Konishi et al. (2002) suggested that while right lateral prefrontal regions became activated in response to the exposure to switching cues (provided by the negative feedback), the homologous left regions became activated during updating of behaviour. Also, the possibility of hemispheric specialization in certain brain regions has received some support with structures such as the right IFJ playing a role in switching preparation, as revealed by the specific analysis of preparation effects in the meta-analysis by Worringer et al. (2019) or the left IFJ increasing cognitive performance through reward (Hippmann et al., 2019).

Transcranial Magnetic Stimulations (TMS) has offered causal evidence about the contribution of different prefrontal (Hippmann et al., 2019; Muhle-Karbe et al., 2014; Rushworth et al., 2002) and parietal areas (Muhle-Karbe et al., 2014) to preparatory control in task-switching by lowering brain activity. Thus, Muhle-Karbe et al. (2014) found that the application of online inhibitory TMS over the left IFJ increased reaction times in switch trials in an experimental condition that involved the updating of abstract task rules. In addition, TMS inhibition of the left IPS increased the percentage of errors when switching involved remapping stimulus-response associations. The authors interpreted that prefrontal and parietal cortices would implement switch-specific preparation processes operating at two different levels of abstraction (i.e., task-goals and response-sets). However, alternative data have questioned the switch-specific preparatory role of prefrontal and parietal brain regions during task-switching (Bode & Haynes, 2009; Mansfield et al., 2012; Ruge et al., 2013). In this regard, evidence about prefrontal activation during both switch and repeat trials suggests that prefrontal areas could implement more general switch-unspecific mechanisms (Barceló et al., 2008; Braver et al., 2003; Gruber et al., 2006; Jamadar et al., 2010). For instance, the use of fMRI during a task-switching paradigm allowed Gruber et al. (2006) to describe the activation of the FPN (i.e., bilateral premotor cortex, left IFJ, right anterior inferior frontal sulcus and middle frontal gyrus, left frontal eye field, and bilateral IPS) in response to advance preparation (i.e., cues *vs* targets contrast) with no differences being founded between switch and repeat trials. Also, using event-related potentials, Barceló et al. (2008) provided physiological evidence about enhanced fronto-

centrally distributed cue-locked activity in response to informative cues in a task-switching paradigm (compared to analogous irrelevant cues in an oddball control task) irrespective of switch or repeat demands. Importantly, these apparently contradictory evidence could provide relevant insights to discuss about the possible multi-dimensional nature of task preparation itself (Ruge et al., 2013) as well as the dissociable role of different brain structures of the FPN (Nyhus & Badre, 2015; Koechlin & Summerfield, 2007; Badre & D'Esposito, 2009). Unfortunately, no previous TMS studies stimulating other areas within the FPN (e.g., inferior frontal gyrus, medial frontal gyrus, posterior parietal junction, or precuneus) have explored further these alternative ideas.

The aim of this work was to clarify the role of prefrontal and parietal areas supporting preparatory control during task-switching performance in a combined fMRI and TMS study. Performance of a well-known cueing task-switching paradigm using fMRI was analysed to identify brain areas associated to preparatory task-switching; then, reducing excitability of those areas using TMS allowed to analyse its disruptive behavioural effects on this task. Following preceding results (Muhle-Karbe et al., 2014), it was hypothesized that if both prefrontal and parietal cortices implement switch-specific preparation processes, then TMS over these areas should interfere with performance in switch, but not in repeat trials. Alternatively, if the activity of either prefrontal or parietal cortices during task-switching relates to a more general switch-unspecific process, then TMS over these regions would interfere with performance in both switch and repeat trials.

2. Materials and methods

We report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study.

2.1. Participants

A study combining fMRI and TMS techniques in two separate sessions with two different groups of participants was conducted. fMRI activation data were used to determine the most suitable target areas for TMS. Power analyses were conducted on the results from a preceding task-switching TMS study (i.e., Muhle-Karbe, et al., 2014) to determine the minimum number of individuals required to reach a power value (1-beta) above .8. Based on the behavioural data as reported there, the authors reach a big effect size of 1.6 with 14 participants. Given this result, we assumed that 20 or more subjects would guarantee a power of .8 in all our contrast. Twenty healthy university students (mean age 26.8 ± 1.3 years; 12 female) participated in the fMRI study. One participant's imaging data was missed due to a technical problem. Therefore, nineteen participants were included in the fMRI analysis. Each participant underwent a screening interview excluding sensory-motor problems, history of neurological, or psychiatric problems, or substance abuse. Twenty healthy university students (mean age 29.3 ± 6.8 years; 13 female) participated in the TMS study. All of them met the TMS safety criteria (Rossi et al., 2009). They had normal, or corrected to normal, visual acuity, and none were taking any medication with effects over the nervous system, or had history of neurological or psychiatric disorder, or drug/alcohol abuse. Inclusion/exclusion criteria were established prior to data analysis. The study was approved by the Ethics Committees of both the Universitat Oberta de Catalunya, and the Gregorio Marañón University Hospital. All participants gave written informed consent to participate in the study following the Declaration of Helsinki. No parts of the study procedures were pre-registered in a time-stamped, institutional registry prior to research being conducted.

2.2. Experimental task

The experimental task-switching paradigm was inspired by the classical numerical judgment task by Allport et al. (1994). One advantage of using this task, as compared to more complex task-switching paradigms, is the symmetry in the difficulty and cognitive demands of the two different subtasks involved. Thus, reducing task demands to two numerical judgments may help avoid the risk of each subtask activating different task-specific brain areas, as demonstrated previously (Shi et al., 2014). Individuals were instructed to respond to target stimuli centred on the screen (a number between 1 and 9, excluding 5) according to one of two possible task rules: odd/even or >5/<5 (see Fig. 1). Task rules were indicated on the basis of a trial-by-trial task-cueing procedure being cues presented between 1000 and 2000 msec prior to the target number. This long cue-to-target interval was selected to favour cue-related task preparation and associated switch-related BOLD activation to occur (Ruge et al., 2013). The cues were two different symbols presented during 300 msec duration that appeared centred on the screen: "x" or "+" for the odd/even and >5/<5 tasks, respectively. All the stimuli were presented in white colour over a black background in Arial font with a physical dimension of 1 × 1 inches. The target display remained on the screen for 300 msec with a response time limit of 3000 msec from the target onset. Participants were instructed to respond to target numbers according to whether the number was odd (left index finger) or even (right index finger) if the preceding cue was the "x" symbol, or whether the number was <5 (left index finger) or >5 (right index finger) if the preceding cue was the "+" symbol. Responses were immediately followed by a 100 msec feedback indicating right, wrong, too fast, or too slow performance. The interval between each response and the next cue adopted a random value between 1000 and 3000 msec (see Fig. 1). Both, speed and accuracy were stressed in the written instructions presented at the beginning of the task. The experimental task was controlled by Presentation software (www.neurobs.com/). These digital materials have been archived in a publicly accessible repository (http://osf.io/pduwr).

Participants from both fMRI and TMS experiment complete blocks of 154 trials organized semi-randomly in 42 series, each containing an initial switch trial followed by a varying number of repeat trials, ranging between 2 and 4. The experimental session lasted around 12 min. Before the experimental task participants practice the task until the experimenter was sure that they had understood the instructions.

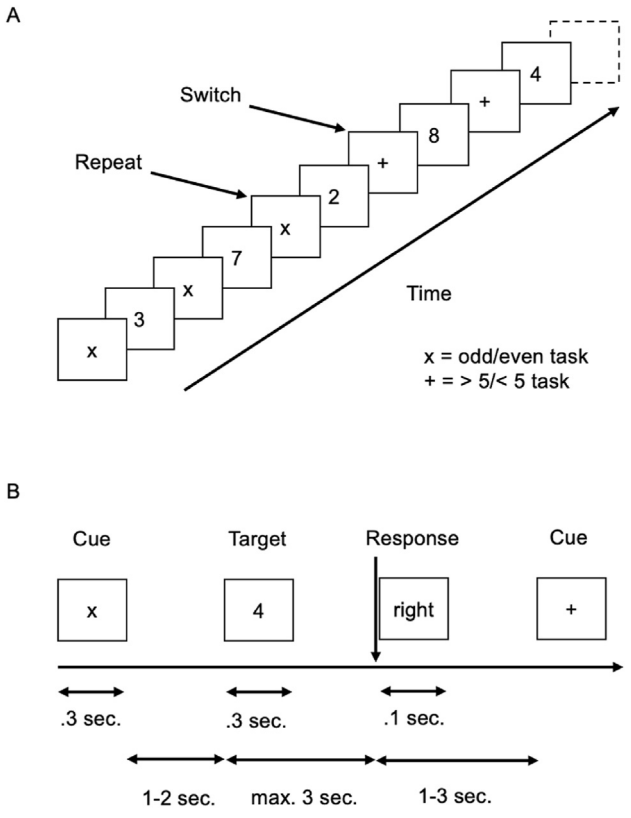

Fig. 1 – Stimulus material and experimental conditions. (A) Schematic of trial sequences illustrating the two experimental conditions being analysed. Switch trials involved a change in task rule as compared with the immediately preceding trial while repeat trials involved using the same rule as before (either odd/even task or >5/<5 task). (B) Each trial consisted of a visual cue ("x" or "+" symbols) followed by a visual target display with one number between 1 and 9, excluding 5. Participants were instructed to respond to target numbers according to whether the number was odd (left index finger) or even (right index finger) if the preceding cue was the "x" symbol, or whether the number was <5 (left index finger) or >5 (right index finger) if the preceding cue was the "+" symbol. Responses were immediately followed by feedback indicating right, wrong, too fast, or too slow performance.

2.3. *fMRI methods*

The fMRI data were acquired on a 3.0T SignaHDx MR scanner (GE Healthcare, Waukesha, WI) using an eight-channel head coil (GE Coils, Cleveland, OH). Head motion was minimized with a vacuum pack system molded to fit each subject. Functional images were obtained with a gradient echoplanar sequence using blood oxygenation level–dependent (BOLD) contrast, each comprising a full volume of 39 contiguous axial slices (3 mm thickness, 0 mm spacing) covering the whole brain. Volumes were acquired continuously with a repetition time (TR) of 2 sec [TE = 25 msec, flip angle = 90, field of view (FOV) = 22 cm, matrix 64 × 64]. A total of 420 scans were acquired for each participant in a single session (14 min run), with the first five volumes discarded to allow for T1 equilibration effects. High-resolution T1-weighted spoiled gradient recall (SPGR) anatomical images were also obtained for each participant (184 1.8-mm-thick axial images, TR = 550 msec, TE = 23 msec, FOV = 24 cm, 256 × 256 matrix).

The Presentation software package (https://www.neurobs.com/) was used for stimuli presentation. Stimuli were presented to participants through optic-fiber-based glasses (MRVision 2000 ultra, Resonance Technology, Inc., Northridge, USA) connected to the stimulation computer. Responses were registered with Lumina LP400 response pads for fMRI.

The data were analysed using a general linear model in SPM12 (Welcome Department of Imaging Neuroscience, London, UK, www.fil.ion.ucl.ac.uk/spm/) implemented in MATLAB R2018a (Mathworks, Inc., Sherborn, MA). Individual scans were i) spatially realigned using six motion parameters (three translations and three rotations) and unwarped to compensate for head-movement (no participants were excluded from fMRI analysis due to excessive movement -point-to-point translation >3 mm and/or rotation >3°-); ii) corrected for differences in slice acquisition time (slice timing correction); iii) spatially normalized and iv) spatially smoothed to reduce noise and to compensate for anatomical inter-subject variability (Gaussian filter of 8 mm FWHM), using standard SPM methods. Population inference was made through a two-stage procedure. At the first level, we specified in a subject-specific analysis where the event-related activity for each voxel, condition and subject was modelled using a canonical haemodynamic response function plus temporal and dispersion derivatives. The analysis of preparation task-switching effects was performed by measuring fMRI cue locked activation in four types of trials modelled separately: switch, 1st repetition, 2nd repetition and last repetition. The switch condition included the initial trial of a series where the current cue indicated to perform a different task than the one performed in the preceding trial (either odd/even or >5/<5). The last repetition condition included the 3rd, and the 4th repetition trials after a switch trial, where the current cue indicated to respond according to the same rule as in the preceding trials. Responses to the different trials were modelled separately with 500 msec duration. Inter-trial intervals contributed to the task baseline. The six motion parameters estimated during preprocessing were included as nuisance regressors. Low-frequency drift was removed using a high-pass filter (.5 cycles/min), and serial correlations were accounted for by modeling the voxel-wise BOLD-signal time series as a first-degree autoregressive process. For each individual, the effect of switch and last repetition conditions was determined (switch > last repetition). Statistical parametric maps of the t-statistic (SPM{t}) were generated for each subject and the contrast images were stored. In a second level random-effects analysis, these images were then combined in a one-sample t-test model (a $p < .001$ at the voxel level was applied in all cases). The surviving activated voxels were superimposed on high-resolution structural magnetic resonance (MR) scans of a standard brain [Montreal Neurological Institute (MNI)]. Anatomical identification was performed with reference to the Talairach Daemon Software (http://www.talairach.org/) and also via XjView8 (http://www.alivelearn.net/xjview/). In

addition, the neuroanatomy atlases by Haines (2011), and Nolte and Angevine (2007) were consulted.

2.4. TMS methods

Before their participation a high-resolution structural MRI was obtained from each participant to rule out any brain abnormalities, to locate the targets for TMS, and to guide the stimulation during the TMS sessions. The MRI was done on a 1.5T scanner (Siemens Magnetom Essenza). Sequences obtained were FSPGR-T1 3D (180 1-mm-thick sagittal slices, TR = 500 msec, TE = 50 msec, 256 × 256 matrix, FOV = 24 cm), SE T1, FSE DP-T2, FLAIR, and diffusion.

All participants underwent three separate sessions in which they received one of the three stimulation conditions: TMS over the right prefrontal area, TMS over the right parietal area or sham stimulation positioning the coil tilted 90° over vertex (control condition). The stimulation sessions were conducted in two consecutive days and the two active conditions (frontal and parietal stimulation) were never applied the same day. At least 4 h separate sessions taking place during the same day to ensure the fading off of the stimulation effects. After each of the stimulation conditions the participants performed the task. The order of the sessions was counterbalanced across participants. The stimulation was performed using a Magstim Super Rapid 2 stimulator (Magstim Company Ltd., Whitland, U.K.) with a 70 mm figure of eight-coil and the position of the coil location during stimulation was guided by a combination of Brainsight (Rogue Research, Montreal Canada) frameless stereotaxic system and Polaris (Northern Digital, Waterloo, ON, Canada) infrared tracking system.

At the beginning of the first session, and before stimulation, active motor threshold (aMT) was individually determined in order to set the appropriate output TMS intensity for each participant. To calculate the aMT, the coil was placed tangentially over the participant's right M1, with the handle positioned 45° backwards. The coil was repositioned until the hot-spot of the left hand first dorsal interosseous (FDI) was located. The aMT was defined as the minimum stimulator output that produced movement in 5 of 10 trials in the FDI when the muscle was gently contracted (approximately 20% of the maximum voluntary contraction). The mean aMT value for the group was 53.4 ± 6.2% of the maximum stimulator output and the intensity applied was the 80% of aMT. After determining aMT, and before stimulation, participants performed practice trials of the experimental task.

Continuous Theta Burst Stimulation (cTBS) was used in order to induce transient decreases of local cortical excitability lasting beyond the stimulation patterns (Huang et al., 2009, 2011). The cTBS protocol consists on a total of 600 TMS pulses grouped in trains of three pulses at 50 Hz, with each train being repeated every 200 msec (5 Hz). The stimulation lasted 40 sec in total and was delivered at 80% of the aMT of each participant (Huang et al., 2009; Rossi et al., 2009). The coil was positioned with the handle oriented backwards in a 45° angle from the midline (orientation), and the stimulation output area tangential to the head of the participant over the target area (tilt). After the cTBS, participants completed the task in a PC with a 17-inch monitor, the response buttons were letters M and Z of the keyboard. As part of the safety protocol, at the beginning and the end of each session, participants completed the Mini Mental State Examination (Folstein et al., 1975), the Beck Depression Inventory (Beck & Steer, 1987), and an ad hoc side effects questionnaire based on Rossi et al. (2009) safety guidelines (see Supplementary material S1) to control for any changes in mood, cognitive functioning or undesired effects of the stimulation.

Targeted cortical areas were localized individually using the high-resolution MRI and the coordinates obtained from the previous fMRI study. The fMRI coordinates were manually adjusted using Brainsight to the individual anatomy moving the target area to the closest cortical gyrus corresponding to IFG and the IPS, in the case, the target was in the inferior parietal lobule. For sham stimulation, the coil was positioned on vertex and tilted 90° to mimic the sound of the stimulation patterns used in the active conditions.

The effect of TMS were analysed by measuring both the percentage of correct responses and RTs to correct trials. Repeated measures ANOVAs or homologous non-parametric tests of differences were conducted where appropriately for RTs and accuracy measures. Consequently, a 3 × 2 repeated measure ANOVA with the factors Area of stimulation (Prefrontal, Parietal, Sham) and Task (switch, repeat) was conducted for RTs analyses. The switch condition included the initial trial of a series where the current cue indicated to perform a different task than the one performed in the preceding trial (either odd/even or >5/<5). The repeat condition included the last trial of a series where cues indicated to respond according to the same rule as in the preceding trials. A significance level of .05 was set for all contrasts. For the analysis of accuracy, a series of non-parametric Friedman tests were employed, assessing the effects of stimulation in different areas across tasks. A Bonferroni-corrected significance level of $p < .05$ was adopted for all tests of simple effects involving multiple comparisons. SPSS version 22.0 statistical software package was used for all the analyses. No analysis code was used.

3. Results

The study data reported here have been archived in a publicly accessible repository (http://osf.io/pduwr). No part of the study analyses was pre-registered in a time-stamped, institutional registry prior to the research being conducted.

3.1. fMRI results

A Student *t* test performed on RTs to switch and repeat correct trials revealed the presence of significant behavioural switch cost [$t(19) = 3.71$; $p < .001$] with an increase of RTs to switch as compared to repeat trials (737 ± 35 *vs* 698 ± 29, respectively). A Student *t* test performed on the percentage of correct responses during switch and repeat trials revealed the presence of marginally significant differences [$t(19) = -1.8$; $p < .088$] in line with a switch cost phenomenon where participants achieved less correct trials after switch cues as compared to repeat cues (94.5% *vs* 96%, respectively).

Functional images were analysed by SPM12 using a general linear model applied at each voxel across the whole brain.

Neuroimaging data from one participant were damaged and unrecoverable for the fMRI analyses, but behavioural data were retained for the analyses of RTs and percentage of correct responses. The analyses allowed to localize those brain areas that modulated their activity during the switch and repeat events. We focused on voxels for which the difference between the responses to the switch events and the repeat conditions was statistically significant. Results showed that cue-related brain activation in the switch > repeat contrast involved the right IFG and the right IFJ, both left and right parietal lobes (intraparietal sulcus), and in the cerebellum (see Table 1; Fig. 2). Results are shown with an uncorrected $p < .001$ but survived a correction at the cluster level for clusters containing the frontal and parietal coordinates selected for TMS stimulation ($p = .012$ and $p = .011$ FWE corrected, respectively; Friston et al., 1994; Woo et al., 2014). The MNI coordinates corresponding to maximum activation at prefrontal and parietal regions during the task performance were x = 48, y = 34, z = 22, and x = 42, Y = −54, z = 58 respectively, and were the two sites selected for TMS stimulation together with the Sham condition. The resulting mean coordinates, after manual adjustment, were x = 47 ± 2, y = 34 ± 1, z = 22 ± 1 for right prefrontal area, and x = 37 ± 2, Y = −55 ± 2, z = 54 ± 3 for right parietal area. The reason for not focusing on additional brain areas was our attempt to minimize the number of experimental conditions and, consequently, the number of sessions in which participants had to perform the same experimental task. This decision is justified, as practicing during multiple sessions has shown to reduce switch costs in different experiments (e.g., Berryhill & Hughes, 2009).

3.2. TMS results

After the TMS sessions none of the participants manifested any major discomfort or side effect produced by the stimulation, as revealed by the pre- and post-questionnaires administered after finishing the task to evaluate the possible cognitive, emotional, and physical undesired effects (see Supplementary material S2).

3.2.1. Reaction times

Given that RTs satisfied the assumptions for ANOVA, a 3 × 2 repeated measures ANOVA with RTs as the dependent variable was performed to compare the effect of TMS in the three different conditions (right IFG, right IPS, and Sham) as a function of Task (switch and repeat). A significant main effect of Area was found [$F(2, 38) = 5.94$; $p < .006$] indicating that, overall, the stimulation of the right IFG resulted in a significant increase of RTs across Task conditions as compared to Sham stimulation ($p < .02$), being the effect of right IPS stimulation only marginal ($p = .078$), and with no differences in RTs between right IFG and right IPS conditions ($p = .514$). The presence of a main effect of Task [$F(1, 19) = 11.75$; $p < .003$] revealed the presence of a significant switch cost effect when switch and repeat trials were compared (694 ± 32 and 658 ± 27 msec, respectively). More importantly was the presence of an Area × Task interaction [$F(2, 38) = 4.25$; $p < .02$]. *Post hoc* analyses of this interaction revealed that while the effect of the right IFG stimulation disrupted RTs in both switch ($p < .02$) and repeat ($p < .04$) conditions as compared to Sham stimulation, the effect of the right IPS stimulation had a specific negative impact over switch trials ($p < .01$) but not in repeat trials ($p < .78$). No other comparison between conditions reached statistical significance ($p > .27$ in all cases; see Fig. 3). Even though, differences in RTs between switch and repeat trials were absent in the Sham condition but remained both in the right IFG and in the right IPS conditions ($p = .34$, $p < .004$ and $p < .003$, respectively).

3.2.2. Accuracy

Subjects performed the task efficiently during the TMS session and typically committed less than 13% errors across each of the three experimental conditions. The average percentage of correct trials across conditions was 95.8%.

Given that the percentage of correct responses did not satisfy the assumptions for ANOVA, non-parametric Friedman tests were used to evaluate the effects of stimulation across tasks in various areas. Results revealed that Area (right IFG, right IPS, and Sham stimulation) did not modulate the number of correct responses, neither in Switch [$\chi^2(2) = .87$, $p < .65$] nor in Repeat trials [$\chi^2(2) = .26$, $p < .88$]. Paired comparisons between tasks at different areas revealed that differences in the percentage of correct responses between switch and repeat trials were absent in the Sham condition but remained both in the right IFG and in the right IPS conditions [$\chi^2(1) = 1.7$, $p = .2$; $\chi^2(1) = 4.8$, $p < .03$; and $\chi^2(1) = 5.4$, $p < .02$, respectively].

Table 1 – Locations and t-values of the main clusters for the Switch > Repeat Last contrast during cues.

Lobe	Region	BA	H	Cluster	x	y	z	t-value
Frontal	Inferior Frontal Gyrus	45	R	539	48	34	22	5.59
	Inferior Frontal Junction	44	R		50	10	24	5.37
	Superior Frontal Gyrus	6	R	27	14	12	54	4.36
Parietal	Precuneus	7	L	137	−10	−76	60	5.04
	Intraparietal Sulcus	40	L	15	−32	−80	48	4.38
	Precuneus	7	R	553	8	−74	48	4.97
	Intraparietal Sulcus	40	R		42	−54	58	4.95
Cerebellum	Cerebellar Tonsil posterior	*	L	161	−22	−64	−32	7.57
	Cerebellar Tonsil posterior	*	R	205	36	−56	−38	5.56

Note: In columns: Lobe, Region, Brodmann area (BA), hemisphere (H), cluster size, MNI coordinates, and t-value.

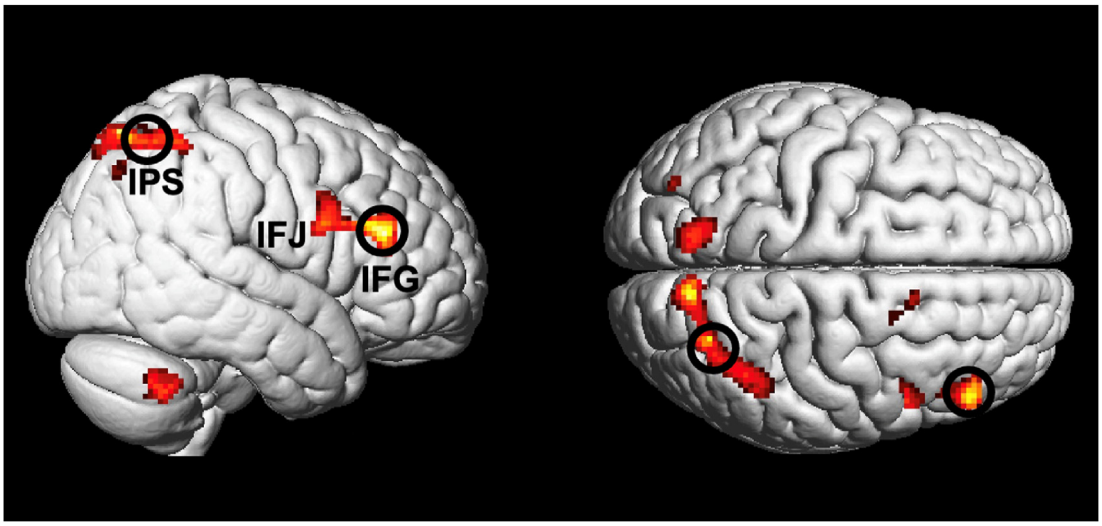

Fig. 2 – fMRI group activation map showing activated brain areas when comparing cues in the Switch > Repeat Last contrast. Three main clusters of activations were identified at the right inferior frontal gyrus (IFG), right inferior frontal junction (IFJ), and both left and right intraparietal sulcus (IPS). The peak coordinates were used as a guide for positioning the coil over the right IFG and the right IPS for TMS. Black circles illustrate mean coordinates for TMS.

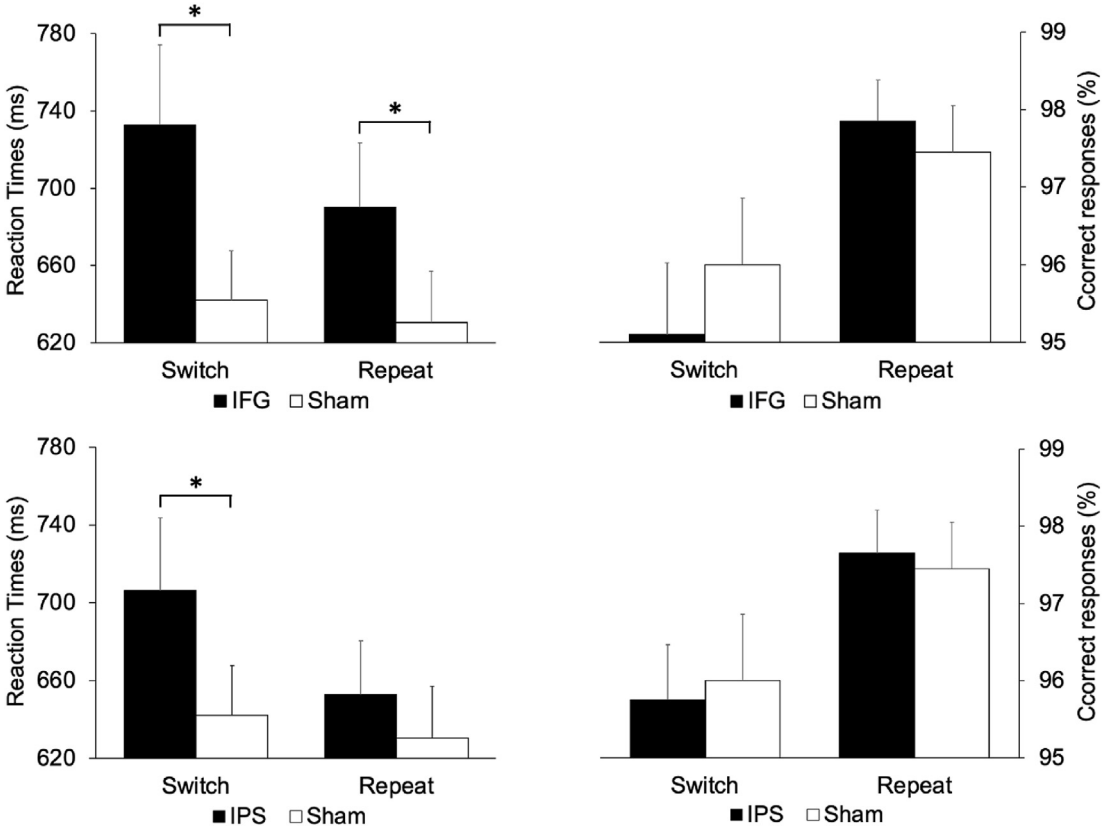

Fig. 3 – Reaction times and percentage of correct responses during task-switching performance in the TMS experiment. Mean reaction times in milliseconds (±S.E.M) and correct responses in percentage (±S.E.M) for the task switch and the task repeat conditions, across the three conditions of TMS: IFG (stimulation of the right Inferior Frontal Gyrus), IPS (stimulation of the right Intraparietal Sulcus), or Sham stimulation.

4. Discussion

The aim of the present fMRI-TMS combined study was investigating the disruptive effect of TMS over specific prefrontal and parietal cortices within a FPN of brain regions previously related to preparatory task-switching. As expected, the results of the fMRI study revealed a behavioural switch cost with an increase in RTs during switch as compared to repeat trials. This behavioural cost was accompanied by an increased fMRI activation in the right IFG, the right IFJ, and bilaterally in the IPS during switch compared to repeat cues (see Table 1, and Fig. 2). These findings are coherent with a large body of evidence suggesting the involvement of a FPN in preparatory process during task-switching paradigms (Dove et al., 2000; Jamadar et al., 2010; Kim et al., 2012; Ruge et al., 2013). Moreover, the pattern of lateralization of the fMRI activations being observed was coherent with the conclusions of one of the largest and more recent existing meta-analysis about the neural correlates of task-switching (Worringer et al., 2019). These authors examine the effect of preparation by dividing the 60 reviewed task-switching studies in two kinds. While "prepared task-switching" included experiments with cue-to-target intervals (CTIs) of 500 msec or more, "unprepared task-switching" included those with CTIs below 500 msec. Importantly, prepared (*vs* unprepared) task-switching was more consistently associated with activation in right IFG, with right IFJ, and left IPS showing negative rank-correlations between activation likelihood and the length of preparatory interval. Taken together these results led us to select the IFG and the IPS as the brain regions for the TMS study, particularly focusing on those in the right hemisphere, as fMRI activation reached higher levels in that hemisphere (see Table 1).

The analyses of the present TMS results revealed that reducing excitability in the right IFG, and right IPS had dissociable behavioural effects, as compared to Sham stimulation. TMS over the right IFG disrupted performance in both switch and repeat trails in terms of delayed responses as compared to Sham condition. In contrast, TMS over the right IPS selectively interfered performance in switch trials (see Fig. 3). However, no behavioural dissociation was evident when the RTs switch cost (i.e., the RT difference between switch and repeat trials) was compared between right IFG and right IPS stimulation conditions, being this cost significant in both cases. To rule out the possibility of a generalized slowing effect due to TMS, additional control analyses were performed (see Supplementary material S3). Specifically, when slowness was statistically controlled using ANCOVA, the dissociation in TMS effects between IFG and IPS remained evident both when comparing the two stimulation sites to the Sham condition, and when comparing the two stimulation sites to each other, thereby dismissing the possibility of a generalized slowing effect. Taken together, and consistent with the initial hypotheses, this partial dissociation would be in line with preceding findings suggesting that the right IPS would be related to the implementation of a switch-specific process (Muhle-Karbe et al., 2014). In addition, present results would also suggest that the right IFG would be involved in a more general switch-unspecific process during task preparation. In fact, previous functional neuroimaging and neurophysiological evidence agree with this interpretation suggesting that preparatory task-switching would involve both general and specific processes associated to certain prefrontal and parietal areas, respectively. For instance, in a study using a hybrid design combining blocked and event-related fMRI, Braver et al. (2003) decompose brain activity associated to sustained and transient components of task-switching. On the one hand, the contrast between mixed task-switching blocks and single-task blocks elicited activation in the right lateral and right medial anterior PFC, that were associated with sustained components of task switching. According to the authors, these components may involve subgoal processing or the episodic retrieval of general task information, common to both switch and repeat trials. On the other hand, the contrast between task-switch and task-repeat trials within mixed blocks elicited activation in regions primarily located in the left hemisphere, including the dorsolateral prefrontal cortex, the ventrolateral prefrontal cortex, and the superior parietal cortex, associated to transient components of task-switching. The authors suggested that while these left prefrontal areas could play a role in lexical/semantic controlled processing, the left superior parietal cortex would be directly involved in task-set reconfiguration or the representation of appropriate stimulus or response representations. In another study integrating event related potentials and fMRI data, Jamadar et al. (2010) found that informative task-switch cues (switch or repeat) evoked larger amplitudes in an early cue-locked positive component as compared to cues providing no information about the next task (non-informative cues). Importantly, this amplitude modulation correlated with fMRI activity in lateral prefrontal cortex (cue informative *vs* cue non-informative contrast), consistent with a general goal activation process. The authors also reported a cue-locked late positivity that was larger for informative switch cues versus repeat cues, whose amplitude correlated with fMRI activity in the posterior parietal cortex (cue switch *vs* cue repeat contrast), compatible with a stimulus-response rule activation process. These findings suggested that the activation of certain regions within the lateral prefrontal cortex would relate more to general preparation processes, than to specific switching operations. Also, in another ERP study, Barceló et al. (2008) found enhanced fronto-centrally distributed cue-locked P3 activity in response to informative cues in a task-switching paradigm irrespective of switch or repeat demands, compared to analogous irrelevant cues in an oddball control task. However, only a late cue-locked P3 component in parietal areas was specifically modulated in response to switch versus repeat equiprobable cues. The authors suggested an association between the fronto-centrally P3 and a general control mechanism related to preparatory process in frontal areas, and between the posterior P3 and a switch-specific reconfiguration process for stimulus-response mapping in parietal areas. Taken together, the above-mentioned evidence and the present results support a multi-component view of anticipatory preparation in task-switching (Ruge et al., 2013). Accordingly, it could be that a general preparation process, such as the retrieval of cue information for goal identification, necessarily during both switch and repeat trials, will recruit the IFG. In this vein, areas in the vicinity of the IFG reported here have been widely

related to different components of memory retrieval. For instance, Nyhus and Badre (2015), associate BA 45 (also referred as mid-ventrolateral prefrontal cortex) to post-retrieval selection needed both to solve competition among multiple memory representations and to align remembered information with current task goals. Also, the application of inhibitory TMS over mid-ventrolateral prefrontal cortex selectively diminishes recall for episodic details in an old/new memory-discrimination task, and lead the authors to attribute a causal role of this area in goal-directed retrieval (Wais et al., 2018). On the other hand, a switch-specific preparation processes such as the translation of abstract task goals into specific action rules or stimulus-response maps for task implementation necessarily during switch trials only, seemed to recruit the IPS. The IPS has been largely related to response selection processes, or more precisely, to stimulus-response mapping. Worringer et al. (2019) interpreted that stronger IPS activation in switch versus repeat trials may reflect the controlled mapping of a given stimulus to the response that is adequate according to the current task-set. IPS projections to ventral premotor areas support the role of this areas in action planning and reorienting of motor attention (Binkofski et al., 1998; Rushworth et al., 2002). The specific area of parietal activation during task-switching may reflect variations based on specific task stimulus attributes (Shi et al., 2014).

It has to be noted that the present findings complement previous knowledge about the role of different prefrontal brain areas during preparatory task-switching (Muhle-Karbe et al., 2014). As mentioned above, these authors found that the application of inhibitory TMS over both the left IFJ and left IPS interfered performance over switch trials only, suggesting that both prefrontal and parietal regions would implement switch-specific preparation processes. On the contrary, the present results revealed that while inhibitory TMS over the right IFG interference performance in both switch and repeat trials, TMS over right IPS produced interference only in switch trials. In addition to the differences in the hemisphere being stimulated in each study (left hemisphere in the Muhle-Karbe et al., 2014 work, and right hemisphere in the present work), a fine-grained anatomical analysis also revealed that two different regions within the inferior prefrontal cortex were stimulated in these two studies. Particularly, the prefrontal brain area stimulated by Muhle-Karbe et al. (2014) (IFJ; MNI: −40, 4, 32, BA 44) was more posterior to the IFG (MNI: 48, 34, 22, BA 45) stimulated in the present study (being both activated in the present fMRI study; Fig. 2). Such a distinction between IFG and IFJ portions of the inferior prefrontal cortex playing differential roles during task-switching performance is coherent with current models suggesting the existence of a hierarchical rostro-caudal organization in lateral prefrontal cortex based in the abstractness of action representations (Koechlin & Summerfield, 2007; Badre & D'Esposito, 2009; O'Reilly, 2010). On the one hand, the IFG (BA 45) would be involved in a general preparatory process such as the retrieval of episodic information for goal selection (Buckner, 2003). This operation would take place at a relatively high level of abstraction any time a cue is presented, and irrespective of switching or repeating task. On the other hand, the IFJ (BA 44) would be involved in a more specific preparatory process such as the updating of task-goals representations (Brass et al., 2005; Derrfuss et al., 2005). Regarding the contribution of parietal brain areas, and following Muhle-Karbe et al. (2014), while the IFJ would provide an initial representation of the task goal that needs to be selected during the next switch trial at a more abstract level, the IPS might specify the resulting stimulus-response mappings, thereby providing a more action-related task representation (Brass et al., 2005; Brass & Von Cramon, 2004). These interpretations fit well with the functional fractionation between episodic and contextual control as proposed by the hierarchical model about the architecture of cognitive control in prefrontal cortex, and about the role of such prefrontal areas in the modulation of posterior brain regions (Koechlin & Summerfield, 2007).

Some potential limitations should be highlighted. Firstly, as it was discussed in the preceding sections, the present results revealed a partial behavioural dissociation in RTs following TMS over right IFG and right IPS compared to sham stimulation. However, this dissociation was not evident when the switch cost was compared across stimulation areas. When the potential slowing effect was statistically controlled by ANCOVA, the behavioural effects during IFG and IPS stimulation exhibited a dissociation with differences being found between repeat trials from IPS and IFG but not between switch trials from IPS and IFG conditions. Although these complementary analyses helped to limit the possibility of a generalized slowing, and despite the main results of this study resembling those from a previous task-switching experiment (Muhle-Karbe et al., 2014), further research should aim to replicate the dissociation reported here. Secondly, although our experimental design successfully identified brain regions responding to the disruptive effects of TMS, using different samples for the fMRI and TMS study might have reduced the robustness of the observations. Thirdly, while a significant switch cost effect was observed during the fMRI session, as well as in the active stimulation conditions (IFG and IPS) of the TMS experiment, RTs during the sham condition were reduced with an absence of behavioural switch cost. This phenomenon is coherent with studies indicating that practicing task-switching over multiple sessions may diminish behavioral switch costs (e.g., Berryhill & Hughes, 2009). It may pose a challenge for TMS studies on task-switching that stimulate multiple target areas, potentially attenuating behavioral effects. Lastly, as mentioned earlier, while the present study complements conclusions drawn from previous TMS studies on the neuroanatomical bases of task-switching (e.g., Muhle-Karbe et al., 2014), it would be interesting in the future to directly test whether the dissociation between the functions of the IFJ stimulated by Muhle-Karbe et al. (2014) and the IFG stimulated in the present study persists under the same TMS and task-switching protocol.

5. Conclusions

In conclusion, the pattern of TMS results observed provides insights into a model of task-switching preparation that encompasses both general and specific reconfiguration processes. Particularly, the present results reveal for the first time that inhibitory stimulation in the right IFG (BA 45) may have caused interference in the retrieval of episodic information for

goal selection during task-switching. This interpretation is coherent with current data about the role of IFG in memory retrieval under high control demands (Buckner, 2003). In addition, our results confirm the implication of the right IPS in task switching behaviour. Specifically, the partial dissociation found is coherent with the purported role of this brain area in more specific mechanisms of goal setting and implementation (Binkofski et al., 1998; Rushworth et al., 2002). Future studies combining fMRI and TMS data might be critical to provide a more complete picture about the complex interaction between brain areas within the frontoparietal network and cognitive control operations during task-switching.

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Open practices

The study in this article has earned Open Data and Open Materials badges for transparent practices. The data and materials studies are available at: http://osf.io/pduwr.

CRediT authorship contribution statement

José A. Periáñez: Writing – review & editing, Writing – original draft, Visualization, Supervision, Project administration, Methodology, Investigation, Formal analysis, Conceptualization. **Raquel Viejo-Sobera:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation. **Genny Lubrini:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis. **Juan Álvarez-Linera:** Writing – review & editing, Resources, Methodology. **Elisa Rodríguez Toscano:** Writing – review & editing, Methodology. **María D. Moreno:** Writing – review & editing, Methodology. **Celso Arango:** Writing – review & editing, Resources, Methodology, Funding acquisition. **Diego Redolar-Ripoll:** Writing – review & editing, Resources, Methodology. **Elena Muñoz Marrón:** Writing – review & editing, Resources, Methodology, Investigation, Funding acquisition. **Marcos Ríos-Lago:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Conceptualization.

Declaration of competing interest

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Supplementary data

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