Fronto-parietal networks underlie the interaction between executive control and conscious perception: evidence from TMS and DWI.

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ABSTRACT

The executive control network is involved in novel situations or those in which prepotent responses need to be overridden. Previous studies have demonstrated that when control is exerted, conscious perception is impaired, and this effect is related to the functional connectivity of fronto-parietal regions. In the present study, we explored the causal involvement of one of the nodes of this fronto-parietal network (the right Supplementary Motor Area, SMA) in the interaction between executive control and conscious perception. Participants performed a dual task in which they responded to a Stroop task while detecting the presence/absence of a near-threshold Gabor stimulus. Concurrently, transcranial magnetic stimulation (TMS) was applied over the right SMA or a control site (vertex; Experiment 1). As a further control, the right Frontal Eye Field (FEF) was stimulated in Experiment 2. Diffusion-weighted imaging (DWI) tractography was used to isolate the three branches of the superior longitudinal fasciculus (SLF I, II and III), and the frontal aslant tract (FAT), and to explore if TMS effects were related to their micro- and macrostructural characteristics. Results demonstrated reduced perceptual sensitivity on incongruent as compared to congruent Stroop trials. A causal role of the right SMA on the modulation of perceptual sensitivity by executive control was only demonstrated when the microstructure of the right SLF III or the left FAT were taken into account. The volume of the right SLF III was also related to the modulation of response criterion by executive control when the right FEF was stimulated. These results add evidence in favor of shared neural correlates for attention and conscious perception in fronto-parietal regions and highlight the role of white matter in TMS effects.

Keywords: conscious perception, DWI, executive control, TMS.

INTRODUCTION

Steadily a big amount of information is reaching our senses, creating a complex, changing, and highly-demanding environment. However, our processing capacities to deal with it are limited. It has been proposed that consciousness may have a role in reducing the noise and increasing the integration of information (Delacour, 1995). Attention is also known to play a key role in the selection of information, especially in crowded environments (Dehaene & Changeux, 2011; Posner, 1994). Following Posner and Petersen's taxonomy of attention (Petersen & Posner, 2012; Posner & Petersen, 1990), the executive control network is one of the three main attentional networks, together with the alerting and orienting networks. Executive control is implemented when situations involve novelty, planning, conflict detection/resolution, and error detection/correction (Norman & Shallice, 1986).

Many authors believe that attention and consciousness are closely related processes, although the nature of such relation is still under debate (Cohen & Dennett, 2011; Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006; Tallon-Baudry, 2012). At the behavioral level, different forms of attention have shown to interact with conscious perception (Chica, Lasaponara, Lupiáñez, Doricchi, & Bartolomeo, 2010; Kusnir, Chica, Mitsumasu, & Bartolomeo, 2011; Petersen, Petersen, Bundesen, Vangkilde, & Habekost, 2017). In particular, executive control modulates conscious perception (Martín-Signes, Paz-Alonso, & Chica, 2018), most likely influencing decision stages of processing (Colás, Capilla, & Chica, 2018; Colás, Triviño, & Chica, 2017). Exploring the neural mechanisms involved in attention and consciousness might provide clues on the nature of their relation. Namely, if attention and consciousness are related processes, shared or partially shared neural correlates are expected (Tallon-Baudry, 2012).

The frontal cortex (together with parietal regions) is crucial for cognitive control (Cocchi, Zalesky, Fornito, & Mattingley, 2013; Cole & Schneider, 2007; Diamond, 2013; Macdonald, Cohen, Stenger, & Carter, 2000) and, according with some theories, also for conscious perception. The global workspace theory (GWT) postulates that distributed large-scale brain networks linking higher visual areas to frontal and parietal cortex are essential for conscious perception (Dehaene et al., 2006; Dehaene, Kerszberg, & Changeux, 1998; Dehaene & Naccache, 2001; Del Cul, Dehaene, Reyes, Bravo, & Slachevsky, 2009; Rees, Kreiman, & Koch, 2002). However, the implication of the frontal regions (and the fronto-parietal network) in conscious perception is in the center of a current debate (Boly et al., 2017; Bor & Seth, 2012; Odegaard, Knight, & Lau, 2017), with some authors arguing that frontal regions are only involved in the processes that emerge after conscious access (e.g. the reporting of the perceptual content or its cognitive manipulation; Tallon-Baudry, 2012).

If both systems (i.e. executive control and conscious perception) share neural resources, an interaction between both processes would be expected in frontal regions. A recent study (Martín-Signes et al., 2018) demonstrated an interaction between executive control and consciousness in the functional connectivity between a set of fronto-parietal regions (including left inferior frontal gyrus –IFG, left anterior cingulate cortex –ACC, left Frontal Eye Field –FEF, left inferior parietal lobe –IPL, right Supplementary Motor Area –SMA, and right superior parietal lobe –SPL). In this functional magnetic resonance imaging (fMRI) study, participants resolved a Stroop task presented at fixation while trying to detect near-threshold Gabor patches presented in the periphery. fMRI data demonstrated that functional connectivity increased between the left IFG-ACC, the left FEF-IPL, and the right SMA-SPL, for congruent trials when near-threshold Gabors were reported as compared to non-reported Gabors. No differences in functional connectivity between these regions were observed on incongruent trials.

According to theories such as the GWT, not only functional connectivity is important for conscious perception. Structural connectivity within the fronto-parietal network may be also key for conscious access. The Superior Longitudinal Fasciculus (SLF) is an extensive longitudinal white matter tract connecting the frontal and parietal lobes. It has been divided in three different branches: SLF I, SLF II and SLF III, labeled from dorsal to ventral. The SLF I extends between the superior parietal lobe and the dorsal and medial parts of the frontal lobe; the SLF II connects the angular gyrus and the posterior regions of the superior and middle frontal gyrus; the SLF III extends between the supramarginal gyrus and the inferior frontal gyrus (Nakajima, Kinoshita, Shinohara, & Nakada, 2019; Rojkova et al., 2016; Thiebaut de Schotten et al., 2011). The SLF has been linked to different attentional functions, including spatial orienting, sustained attention, and executive control in the healthy population (Carretié, Ríos, Periáñez, Kessel, & Álvarez-Linera, 2012; Klarborg et al., 2013; Sasson, Doniger, Pasternak, Tarrasch, & Assaf, 2012, 2013; Thiebaut de Schotten et al., 2011) and in different neurological conditions related with attention or awareness deficits (for example, spatial neglect, Doricchi, Thiebaut de Schotten, Tomaiuolo, & Bartolomeo, 2008; Thiebaut De Schotten et al., 2014; and attention-deficit/hyperactivity disorder, Chiang, Chen, Lo, Tseng, & Gau, 2015; Chiang, Chen, Shang, Tseng, & Gau, 2016; Wolfers et al., 2015). Newly, the microstructure of the right SLF III has been associated with the perceptual contrast needed to perceive near-threshold targets in patients with prefrontal damage (Colás et al., 2019). The neural interaction between conscious perception and different attentional subsystems has also been related to the microstructure of the SLF (Chica, Thiebaut de Schotten, Bartolomeo, & Paz-Alonso, 2018; Martín-Signes et al., 2018; Martín-Signes, Pérez-Serrano, & Chica, 2017).

The aim of this study was to explore the causal role of a frontal region in the interaction between executive control and conscious perception by using transcranial magnetic stimulation (TMS). To this aim, participants performed a Stroop task (to manipulate executive control, Stroop, 1935) concurrent with a detection task of near-threshold Gabor stimuli (see Colás et al., 2017). Based on previous correlational fMRI findings (Martín-Signes, Paz-Alonso, & Chica, 2018), the right SMA was selected as a target region (Experiment 1) because its functional connectivity with the right SPL demonstrated an interaction between executive control and conscious perception. The SMA has been traditionally linked to the motor control domain (Brass, 2002; Luppino, Matelli, Camarda, & Rizzolatti, 1993), however, especially the anterior part, is also linked to cognitive control functions (Miller & Cohen, 2001; Nachev, Kennard, & Husain, 2008). The right FEF was selected as an active control region (Experiment 2), because this region was related to conscious perception but not to the interaction between executive control and conscious perception. Based on previous observations demonstrating the role of the SLF in conscious perception, executive control, and the interaction between both processes (and its implication in other attentional systems), we also explored the role of the three branches of the SLF in the TMS effects over the expected behavioral interaction (as done before, Martín-Signes et al., 2017) .

If our results show a causal role of the right SMA in the interaction between executive control and consciousness, this would add evidence in favor of shared neural correlates for executive control and conscious perception (Tallon-Baudry, 2012). The implication of a frontal region (i.e. the SMA) and its relation with the microstructural properties of SLF (a fronto-parietal tract) would constitute new evidence for the involvement of the fronto-parietal network in conscious perception.

EXPERIMENT 1: RIGHT SMA vs. VERTEX

METHODS

Participants

G*power (Faul, Erdfelder, Lang, & Buchner, 2007) was used to calculate sample size based on the effect size of a previously observed interaction between alerting and TMS region in a similar experiment (Martín-Signes et al., 2017; $\eta^2p = 0.38$). We calculated sample size for a F test (interaction between Congruency and TMS region, $\alpha = 0.05$; Power = 0.95). A sample of 24 participants was required. Therefore, 24 right-handed volunteers (12 females, mean age 24 years, standard deviation [SD] = 3.60) took part in the study.

Participants were unexperienced with the task and reported to have normal or corrected-to-normal vision, normal-color discrimination, and Spanish as their native language. Participants had no neurological or psychiatric conditions and followed all the safety requirements to undergo MRI and TMS studies (Rossi, Hallett, Rossini, & Pascual-Leone, 2012). They signed an informed consent to participate in the experiment and received a monetary compensation for their time and effort (10 Euros/hour). The study was reviewed and approved by the Ethical Committee of the University of Granada and was carried out according to the recommendations of Helsinki Declaration.

Apparatus and Stimuli

The paradigm and procedure was an adaptation of the one employed in Martín-Signes et al., 2018. E-prime software was used to control the presentation of stimuli, timing operations, and behavioral data collection (Schneider et al., 2002). Images were presented in a computer screen (Benq T903, 19’’ wide, 1280x1024, 60 Hz) while participants where sited at an approximate distance of 77 cm. Two markers (3° height × 5.3° width) and a central fixation point (0.4°×0.4°) were displayed against a gray background at the beginning of the trial. Each marker consisted of a black square outline, placed 4.5° to the left and right of the fixation point. Spanish words for blue (“azul”, 0.4° height × 1.6° width), green (“verde”, 0.4° height × 2° width), red (“rojo”, 0.4° height × 1.6° width), and yellow (“amarillo”, 0.4° height × 3° width) colors were presented 0.6° above the fixation point (Fig. 1A). Words were colored either in blue, green, red, or yellow. Trials were sorted as congruent when the word meaning and the word color matched, and as incongruent when the word meaning and the word color were different. Response latencies to the Stroop task were collected using an ATR 20 microphone with low impedance connected to a Serial Response Box (Psychology Software Tools, Schneider, 1995).

The target was a Gabor stimulus that could appear inside of one of the lateral boxes. Matlab 8.1 (http://www.mathworks.com) was used to create 100

Gabor stimuli (4 cycles/deg spatial frequency, 1.8° in diameter, SD of 0.1°), with a maximum and minimum Michelson contrast of 0.92 and 0.02, respectively. Gabor contrast was manipulated before the experimental task in order to adjust the percentage of consciously perceived targets to ~50% (see Procedure).

Procedure

The timing and sequence of the events presented in a trial are depicted in Figure 1A. In each trial, participants were presented with a color word and a Gabor stimulus (except for catch trials, in which the Gabor was not presented). Participants were required to perform two consecutive tasks. First, they had to discriminate the color of the word as fast and accurately as possible. Participants responded to this task orally and response latencies (i.e. reaction times, RTs) were collected through the microphone. For the computation of the accuracy, the experimenter recorded the participant's responses using four keys of the keyboard (“1” for yellow, “2” for red, “4” for blue and, “5” for green). Second, participants had to report if they consciously detected the appearance of the Gabor. They were asked to respond as accurately as possible and only when they were confident about their perception. The response was given by choosing one of the two arrow-like stimuli (>>> or <<<) pointing to the two possible locations of target appearance (right or left box). The arrows were presented one above the other, with their position randomized in each trial. Participants were required to indicate the location of the target, with the right hand. They had to press an upper key (“K”), corresponding to the upper arrow or a lower key (“M”) corresponding to the bottom arrow. If they had not perceived the Gabor, they were asked to press the space bar. Participants were explicitly instructed to fixate the central plus sign throughout all the experiment.

Each participant performed two experimental blocks, one for the right SMA stimulation and one for the control TMS site (vertex, see Fig.1B). The order of the SMA and vertex blocks was counterbalanced between participants. Each block consisted in 240 trials (accounting for a total of 480 trials for the experiment). The proportion of Congruent-Incongruent Stroop trials was 70-30%, respectively. The Gabor was present on 66% of the trials, and absent on the remaining 34% of the trials (catch trials).

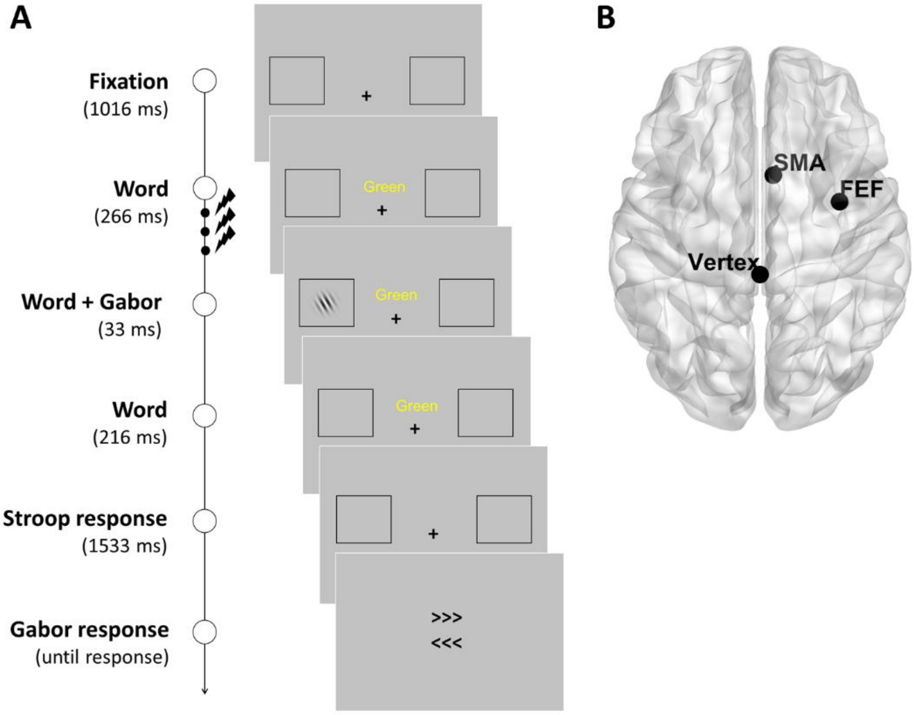

Figure 1. (**A**) Representation of the sequence of events on a given trial. The image shows a Stroop incongruent trial with a Gabor present on the left location. Thunderbolt symbols indicate the burst of TMS pulses. (**B**) Representation of the TMS sites for Experiment 1 (Right Supplementary Motor Area, SMA), Experiment 2 (Right Frontal Eye Field, FEF), and the control TMS site for both experiments (Vertex) in an axial brain view.

MRI data acquisition

Structural images were collected on a 3-T Siemens Trio MRI scanner at the Mind, Brain, and Behavior Research Center (CIMCYC, University of Granada), using a 32channel whole-head coil. High-resolution T1-weighted anatomical images (Repetition Time [TR] = 2530ms, Echo Time [TE] = 3.5ms, flip angle = 7°, slice thickness = 1mm, field of view = 256mm) were collected. Additionally, a total of 70 near-axial slices were acquired using a sequence fully optimized for tractography of diffusion-weighted imaging (DWI) providing isotropic 2-mm resolution and coverage of the whole head with a posterior–anterior phase of acquisition (TR = 8400ms and TE = 88ms). At each slice location, 6 images were acquired with no diffusion gradient applied and 60 diffusion-weighted images in which gradient directions were uniformly distributed in space. The diffusion weighting was equal to a b-value of 1500 s/mm^2.

TMS procedure

TMS was delivered by means of a biphasic repetitive stimulator (Super Rapid 2, Magstim, Whitland UK) and a 70-mm figure-of-eight coil (Magstim, Whitland UK) positioned at ~45° respect to the scalp. The TMS coil was controlled by a robotic arm (TMS Robot, Axilum Robotics) and a TMS neuronavigation system (Brainsight, Rogue Systems, Montreal, Canada) with the capacity to estimate and track in real time the relative position, orientation, and tilting of the coil on the sectional and 3D reconstruction of the participant’s MRI. The TMS robot guaranties the accurate stimulation of a given brain region during the experiment, by automatically adjusting its position if a movement larger than 5 mm was detected.

On each trial, a burst of three TMS pulses were applied at 40 Hz simultaneously to the presentation of the Stroop word and with a total duration of

56 ms. As previously done elsewhere (Bourgeois, Chica, Valero-Cabré, & Bartolomeo, 2013; Chica, Bartolomeo, & Valero-Cabré, 2011), we attempted to use a fixed TMS intensity of 80% of the Maximum Stimulator Output (MSO). This intensity was adjusted for each participant to avoid discomfort, and face or hand muscular movements. The mean applied TMS intensity was 69% of MSO (SD = 7.35). For each participant, the same TMS intensity was used for the right SMA and the vertex stimulation. The right motor threshold (MT) was determined for each participant at the beginning of the experiment (see Martín-Arévalo et al., 2019 for a detailed explanation of the procedure). The mean right MT was 65% of MSO.

Scalp coordinates for the stimulation sites were located by using the native space of each participant's T1. The TMS stimulation site was the right SMA (Montreal Neurological Institute [MNI] coordinates: x = 6, y = 11, z = 55), which was extracted from a previous fMRI study (Martín-Signes, Paz-Alonso, & Chica, 2018) (see Fig. 1B). We checked the exact location of the stimulated region in each participant's brain: for 12 participants the coordinates overlapped with the pre-SMA, for 8 participants with the SMA-proper, and for 4 participants the coordinates landed in between both regions. Given the slight variability in the location of the coordinates in each participant's brain, and the spatial resolution of TMS (Jahanshahi & Rothwell, 2000), we can conclude that the SMA complex (i.e. pre-SMA and SMA-proper) was stimulated. From now on, we will refer to it as the SMA for the sake of simplicity. The control stimulation site was the vertex (MNI coordinates: x = 0, y = −34, z = 78; Martín-Arévalo et al., 2019), which was not expected to induce any specific behavioral effects (Jung et al., 2016).

DWI tractography analysis

In each slice, DWI data were simultaneously registered and corrected for subject motion, and eddy current and echo planar imaging distortions, adjusting the gradient accordingly (ExploreDTI, Irfanoglu, Walker, Sarlls, Marenco, & Pierpaoli, 2012; Leemans, Jeurissen, Sijbers, & Jones, 2009; Leemans & Jones, 2009). Spherical deconvolution was then performed employing the damped Richardson–Lucy deconvolution algorithm (Dell'Acqua et al., 2010) with the Software StarTrack (http://www.natbrainlab.com). Algorithm parameters were $\alpha = 2$, algorithm iteration = 400, and $\eta = 0.06$ and $v = 8$ as regularization terms (Dell'Acqua, Simmons, Williams, & Catani, 2013). Whole-brain deterministic tractography was performed using a modified Euler tractography algorithm (angle threshold = 45º, absolute hindrance modulated [HMOA] threshold = 0.1, and relative threshold = 10%).

Individual dissections of the tracts were carried out with the software TrackVis (Wang, Benner, Sorensen, & Wedeen, 2007). The 3 branches of the SLF (on the left and the right hemispheres) were isolated using a multiple region of interest (ROI) approach. Three frontal ROIs around the white matter of the superior, middle and inferior frontal gyri and a ROI around the white matter of the parietal lobe were delineated. Streamlines of the arcuate fasciculus projecting to the temporal lobe were excluded by drawing a no-part ROI in the temporal white matter. Cingulate fibers were distinguished from the SLF I by delineating the frontal ROI above the cingulate sulcus (See Rojkova et al., 2016; Thiebaut de Schotten et al., 2011 for a detailed explanation of the method). The HMOA, an index employed as a surrogate for tract microstructural organization (Dell'Acqua et al., 2013), was extracted from each dissected tract. The mean HMOA is defined as the absolute amplitude of each lobe of the fiber orientation distribution and considered highly sensitive to axonal myelination, fiber diameter, and axonal density. Also, following the suggestion of a reviewer, two measures of the macroscopic properties of the tracts (i.e. volume and number of tracks) were extracted.

Behavioral Data Analysis

Mean accuracy and RTs for the Stroop task were analyzed by means of two repeated-measured analysis of variance (ANOVA) with the factors of Region (SMA and vertex) and Congruency (congruent and incongruent). Stroop RTs shorter than 350 ms (10.41%[1] of the trials, SD = 0.17) and errors in the Stroop task (1.13% of the trials, SD = 0.01) were eliminated from the RTs analysis. Additionally, 5 participants were excluded from the RTs analysis[2]. Stroop task analyses included only Gabor present trials. Errors localizing a consciously seen Gabor (1.12% of the trials, SD = 0.01) were excluded from all the analyses.

We analyzed participants’ responses to the conscious detection task using the Signal Detection Theory (SDT, Abdi, 2007). We computed the mean percentage of seen targets when the Gabor was present (hits), and when the Gabor was absent (false alarms; FA). Non-parametrical indices of perceptual sensitivity (A’) and response criterion (Beta’’) were computed.

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[1] This relatively high percentage of RTs under 350 ms was caused by an interference of the TMS sound with the microphone. During the trial, the microphone was opened after the TMS pulses were applied to capture the participant´s response. However, in some of the trials, the sound of the TMS pulses reverberated for a longer time and thus, interfered with the recording of the microphone. This problem affected the first 13 participants but it was solved for the rest of the sample. [2] Participants with >30% of the trials affected by the interference of the TMS sound (see footnote 1) were excluded for the RTs analysis.

A’= $0.5 + \frac{(\text{Hits}-\text{FAs})*(1+\text{Hits}-\text{FAs})}{4*\text{Hits}*(1-\text{FAs})}$; Beta’’= $\frac{\text{Hits}*(1-\text{Hits})-\text{FAs}*(1-\text{FAs})}{\text{Hits}*(1-\text{Hits})+\text{FAs}*(1-\text{FAs})}$

A’ values usually range between 0.5 (the signal cannot be distinguished from the noise) and 1 (perfect performance). For Beta”, values close to 1 indicate a conservative criterion, whereas values close to − 1 indicate a non-conservative criterion (Stanislaw & Todorov, 1999). SDT analyses included only correct response Stroop trials. SDT indices were submitted to two repeated-measures ANOVAs with the factors of Region (SMA and vertex) and Congruency (congruent and incongruent).

We were interested in exploring the role of the three branches of the SLF in the TMS effects over the interaction between executive control and conscious perception. We performed two multiple linear regression with the forward method, to predict the interaction effects on A’ and Beta’’. As predictors, we used the mean HMOA of the right and left SLF I, II and III. To calculate the interaction indices, we subtracted the congruent minus incongruent condition for SMA stimulation minus the congruent minus incongruent condition for the vertex stimulation. In the index, the larger the value, the larger the TMS effect over the congruency effect. One participant was excluded from the linear regression analysis of Beta’’ index due to an outlier value (>3 SD from the mean).

RESULTS

For the Stroop task, the expected Congruency effect was observed. Mean accuracy was significantly higher for congruent compared with incongruent trials, F(1, 23) = 39.23, MSE = 0.0005, $p < 0.001$, $\eta^2p = 0.63$, and RTs were also shorter for congruent compared with incongruent trials, F(1, 18) = 36.16, MSE = 5019, p

< 0.001, $\eta^2p = 0.67$ (Figure 2C-D). No effects of Region or interactions were found (all ps > 0.425).

For the Gabor detection task (Figure 2A-B), perceptual sensitivity was enhanced for congruent compared with incongruent trials, $F(1, 23) = 6.65$, $MSE = 0.0003$, $p = 0.017$, $\eta^2p = 0.22$). However, no effects of Region or interactions were found (all ps > 0.344). Moreover, no significant results were observed when response criterion (Beta'') was analyzed (all ps > 0.121).

The results of the regression analysis ($F(1,22) = 5.826$, $p = 0.025$, $R^2 = 0.209$) showed that the right SLF III was a significant predictor for the TMS effects over perceptual sensitivity (A' index), $\beta = -0.458$, $p = 0.025$. Similarly ($F(1,21) = 5.799$, $p=0.025$, $R^2 = 0.216$), the right SLF III was also a significant predictor for the TMS effects over response criterion (Beta'' index), $\beta = -0.465$, $p = 0.025$. This suggests that participants with lower mean HMOA of the right SLF III had larger TMS effects both in A' and Beta'' indices (see Fig. 3A-B).

We then replicated the repeated-measures ANOVAs for A' and Beta'' including the significant predictor as a covariate (i.e. the mean HMOA of the right SLF III). When doing so for the A' analysis, the interaction between Region and Congruency reached significance, $F(1, 22) = 6.20$, $MSE = 0.0001$, $p = 0.021$, $\eta^2p = 0.22$, and this interaction depended on the mean HMOA of the right SLF III, $F(1, 22) = 5.83$, $MSE = 0.0001$, $p = 0.025$, $\eta^2p = 0.21$. TMS over the SMA (as compared with the vertex condition) impaired conscious perception for incongruent Stroop trials. However, this effect was mainly observed in participants with low integrity values of the right SLF III (Figure 3C-D). For Beta'', the interactions between Region and Congruency, and between Region x Congruency x right SLF III did not reach significance ($F(1, 22) = 4.04$, $MSE =$

0.059, $p = 0.057$, $\eta^2p = 0.15$, and $F(1, 22) = 4.21$, $MSE = 0.059$, $p = 0.052$, $\eta^2p = 0.16$, respectively).

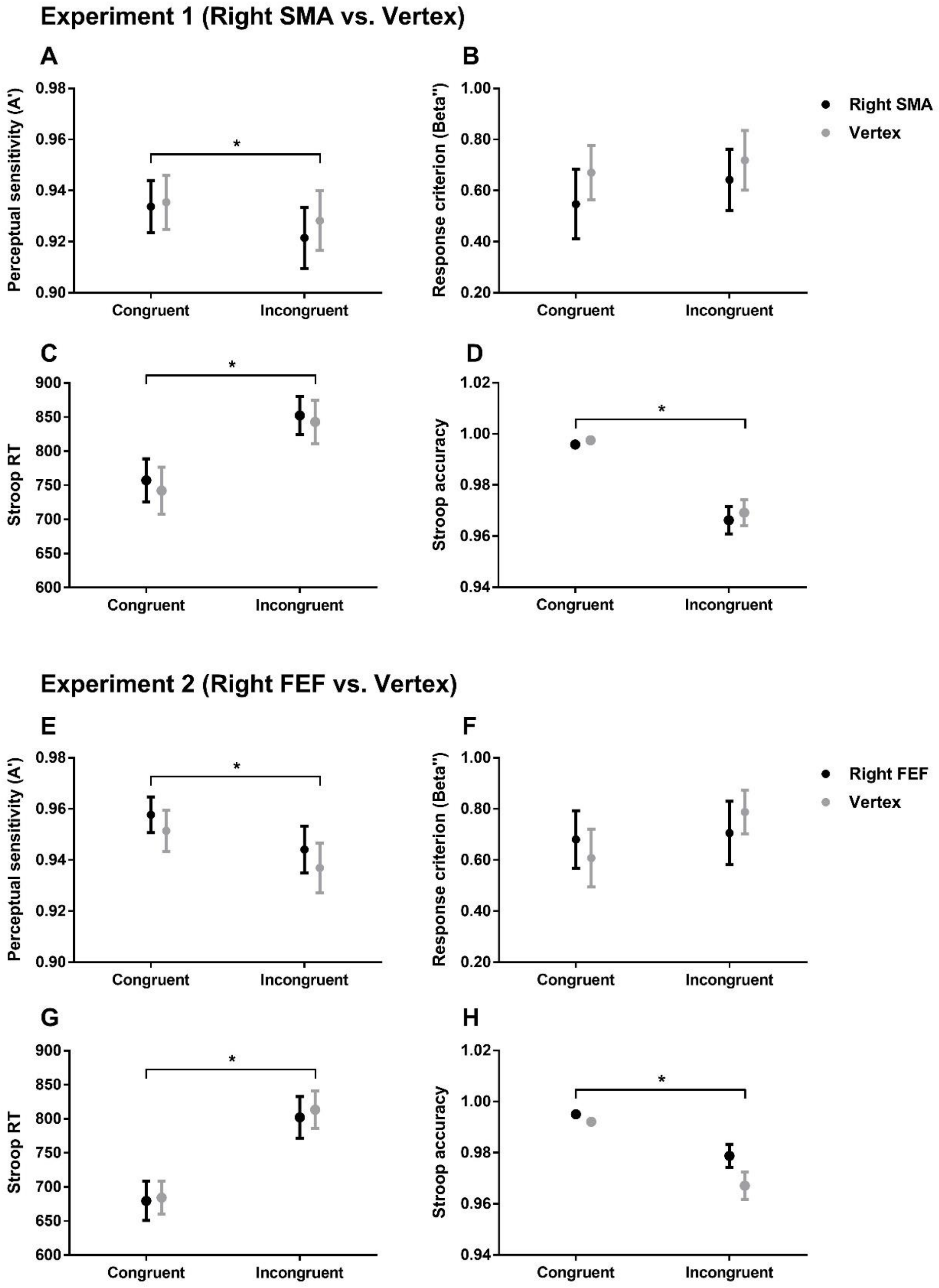

Figure 2. Congruency effect for (**A, E**) perceptual sensitivity, (**B**, **F**) response criterion, (**C**, **G**) Stroop reaction time (RT, in ms), and (**D**, **H**) Stroop

accuracy for Experiments 1 and 2. Errors bars represent standard errors of the mean. Asterisks represent significant Congruency main effects.

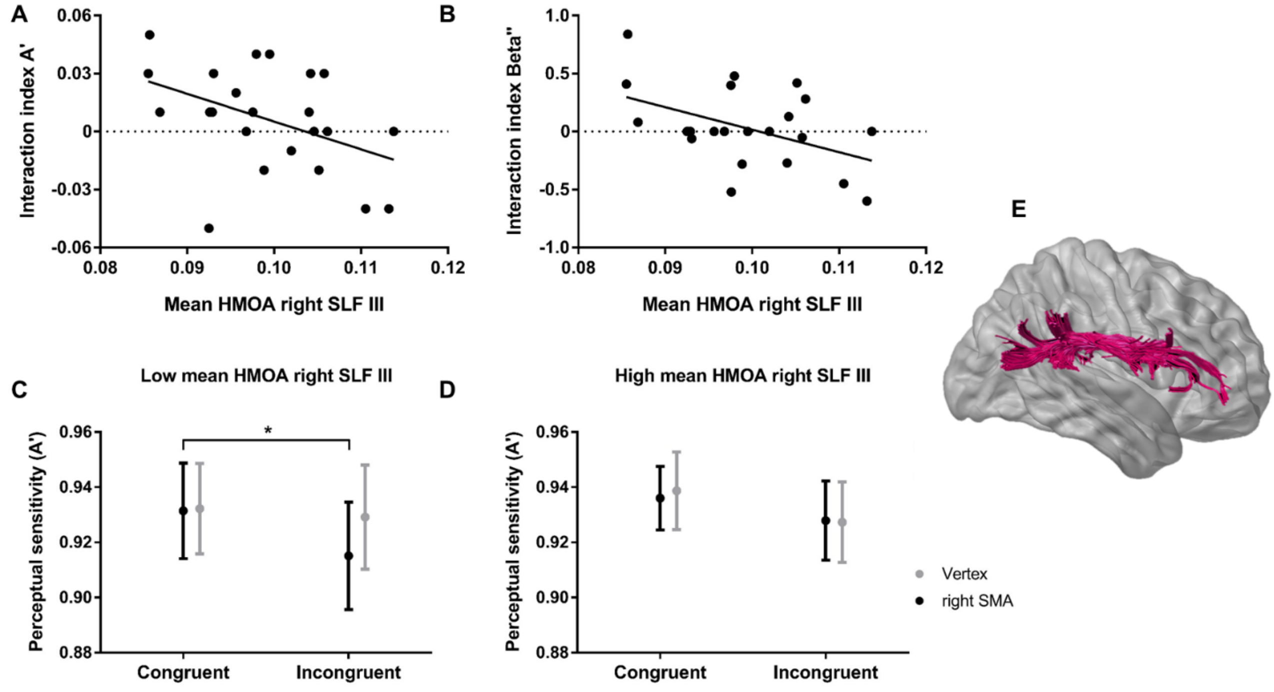

Figure 3. (**A**, **B**) Correlation between the mean HMOA of the right SLF III and the SMA-TMS effect (Experiment 1) for perceptual sensitivity and response criterion. The black line represents the best fit of the data. (**C**, **D**) For experiment 1, Region and Congruency interaction for perceptual sensitivity for participants with a mean HMOA of the right SLF III under the median (low mean HMOA) and over the median (high mean HMOA). Errors bars represent standard errors. Asterisk represent a significant comparison between congruent and incongruent condition when the right SMA was stimulated, $t = 3.66$, $p = 0.004$. (**E**) Representation of a virtual in vivo dissection of the SLF III of the right hemisphere using deterministic tractography.

Post hoc DWI tractography analysis

Additional tracts. Following the suggestion of a reviewer, the frontal aslant tract (FAT) and the SPL-SMA complex of the SLF I were delineated and included in the DWI tractography analysis. In order to test the relation between the new tracts and behavioral and TMS effects, we followed the same pipeline that was employed for the SLF analysis (see Methods section).

FAT is a recently defined tract that runs from the medial part of the superior frontal lobe (i.e. pre-SMA, SMA-proper, and ACC) to the posterior IFG (Catani et al., 2012; Thiebaut de Schotten, Dell'Acqua, Valabregue, & Catani, 2012). Thus, it connects the targeted area with the terminations of the SLF III. This tract might be important for language, speech, and executive control (Dick, Garic, Graziano, & Tremblay, 2019). The left and right FAT were delineated by using a multiple ROI approach (Fig 4E; Catani et al., 2012). A 6 cm-sphere ROI was placed in the SMA complex, and a 5 cm-sphere ROI was placed in the triangularis and opercularis parts of the IFG. We performed two regression analyses with the interaction index for A' and Beta'' using the mean HMOA of the left and right FAT as predictors. The results of the regression analysis (F(1,22) = 5.44, p = 0.029, R^2 = 0.198, and F(1,21) = 5.201, p = 0.033, R^2 = 0.199, respectively) showed that the left FAT was a significant predictor for the TMS effects over perceptual sensitivity (A' index), β = -0.445, p = 0.029, and response criterion (Beta''), β = -0.446, p = 0.033 (See Fig. 4A-B). When including the mean HMOA of the left FAT as a covariate for the repeated-measures ANOVA for A' and Beta'', the interaction between Region and Congruency reached significance only for A', F(1, 22) =5.82, MSE = 0.0001, p = 0.025, η^2p = 0.21, and this interaction depended on the mean HMOA of the left FAT, F(1, 22) = 5.44, MSE = 0.0001, p = 0.029, η^2p = 0.20. TMS over the SMA (as compared with the vertex condition) impaired conscious perception for incongruent Stroop trials. However, this effect was mainly observed in participants with low integrity values of the left FAT (Figure 4C-D).

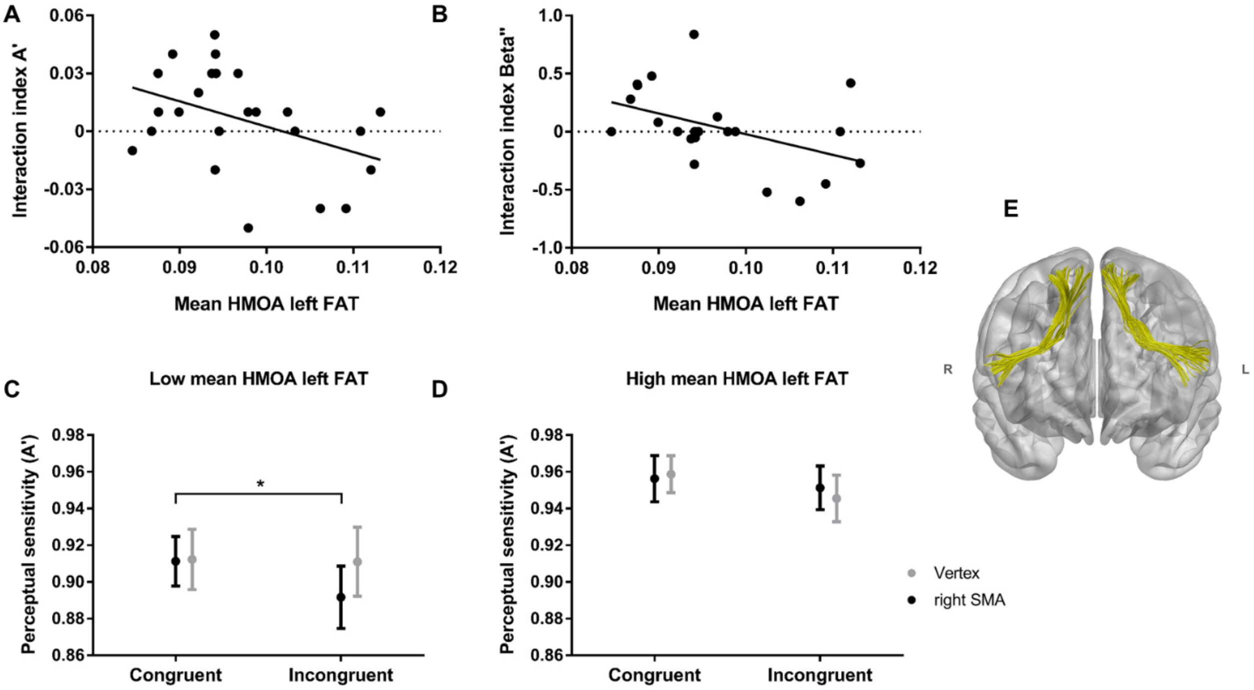

Figure 4. (**A**, **B**) Correlation between the mean HMOA of the left FAT and the SMA-TMS effect (Experiment 1) for perceptual sensitivity and response criterion. The black line represents the best fit of the data. (**C**, **D**) For experiment 1, Region and Congruency interaction for perceptual sensitivity for participants with a mean HMOA of the left FAT under the median (low mean HMOA) and over the median (high mean HMOA). Errors bars represent standard errors. Asterisk represent a significant comparison between congruent and incongruent condition when the right SMA was stimulated, t = 2.29, p = 0.043. (**E**) Representation of a virtual in vivo dissection of the right and left FAT using deterministic tractography.

The SLF I connects the superior parietal lobe with the anterior cingulate cortex, by passing thought the SMA complex (Bozkurt et al., 2017, 2016; Jang & Hong, 2012). We delineated this SPL-SMA segment of the right and left SLF I by using a multiple ROI approach. We employed a parietal ROI (see dissection of the SLF) and a 6 cm-sphere over the SMA complex. We then performed two regression analyses with the interaction index for A’ and Beta’’ using the mean HMOA of the left and right SPL-SMA complex. The results of the regression analysis ($F(1,19) = 4.62$, $p = 0.045$, $R^2 = 0.196$) showed that the mean HMOA of the right SPL-SMA complex was a significant predictor for the TMS effects over response criterion (Beta’’ index), $\beta = -0.442$, $p = 0.045$. But, when including this predictor as a covariate for the repeated measures ANOVA for Beta’’, no significant interactions between region and congruency were found (all ps > 0.206).

Analysis of the macroscopic properties. Following an identical pipeline to the microscopic analysis (i.e. mean HMOA), we analyzed the relation between the volume of all dissected tracts and the TMS effects over the behavioral measures (A’ and Beta’’ indices). Although the number of tracks was also extracted, it was not analyzed here. We refer to the available data of this work for further analysis (https://osf.io/g8ue5/?view_only=b54ba6ec57b54810b92a220f402da6e8).

The results of the regression analysis for the SLF ($F(1,21) = 5.03$, $p = 0.036$, $R^2 = 0.193$) showed that the volume of the left SLF I was a significant predictor for the TMS effects over response criterion (Beta’’ index), $\beta = -0.440$, $p = 0.036$. But, when including this predictor as a covariate for the repeated measures ANOVA for Beta’’, no significant interactions between region and congruency were found (all ps > 0.463). No other significant models were found for any of the tracts for any of the behavioral measures (all ps > 0.073).

EXPERIMENT 2: RIGHT FEF VS. VERTEX

METHODS

Participants

24 right-handed volunteers (12 females, mean age 23 years, SD = 2.87) took part in the study.

Apparatus and Stimuli, Procedure and Analysis

These were identical to Experiment 1 with the exception of the TMS target (Fig. 1B). The TMS stimulation sites were the right FEF (MNI coordinates: $x = 36$, $y = -1$, $z = 53$), which was extracted from a previous fMRI study (Martín-Signes, Paz-Alonso, & Chica, 2018), and the vertex. The mean TMS intensity applied was 60% of MSO (SD = 6.95). The mean right MT was 66% of the MSO. Stroop RTs shorter than 350 ms accounted for 0.60% of the trials (SD = 0.01). Errors in the Stroop task constituted 1.21% of the trials (SD = 0.01) and errors localizing a consciously seen Gabor 1.30% of the trials (SD = 0.03). DWI data from two participants could not be collected (N = 22).

RESULTS

For the Stroop task, mean accuracy was also significantly higher for congruent compared with incongruent trials, $F(1, 23) = 22.33$, $MSE = 0.0005$, $p < 0.001$, $\eta^2p = 0.49$, and RTs were shorter for congruent compared with incongruent trials, $F(1, 23) = 140.85$, $MSE = 2691$, $p < 0.001$, $\eta^2p = 0.86$ (see Fig. 2G-H). We also found an effect of Region for mean accuracy, $F(1, 23) = 6.31$, $MSE = 0.0002$, $p = 0.019$, $\eta^2p = 0.22$, with better performance when TMS was applied over the right FEF as compared to the vertex condition. No other effects or interactions were found (all ps > 0.174).

For the Gabor detection task, we found a significant Congruency effect over perceptual sensitivity (A'), $F(1, 23) = 12.04$, $MSE = 0.0004$, $p = 0.002$, $\eta^2 p = 0.34$, with better performance for congruent than incongruent trials. No significant effects over response criterion (Beta'') were found (all ps > 0.225, see Fig. 2E-F).

The linear regression analysis including the mean HMOA of the right and left SLF I, II and III as predictors, revealed no significant models to predict the TMS effect for neither of the two dependent variables tested (i.e. behavioral indices of A' and Beta''). To confirm that the TMS effects found in Experiment 1 were region-specific, we replicated the repeated-measures ANOVAs for A' and Beta'' including the mean HMOA of the right SLF III as a covariate. Results showed that the interaction between Region and Congruency was still not significant neither for A' nor for Beta'' (all ps > 0.605). We also conducted Pearson correlations between the mean HMOA of the right SLF III and the interaction index for A' and Beta''. No significant correlations were found between the variables (all ps > 0.747).

Post hoc DWI tractography analysis.

Additional dissections. As done for Experiment 1, left and right FAT and SPL-SMA complex of the SLF I were incorporated to the DWI tractography analysis. The linear regression analyses revealed no significant models to predict the TMS effects for neither of the two dependent variables tested (i.e. behavioral indices of A' and Beta'') for any of the tracts (all ps > 0.129).

Analyses of the macroscopic properties. As done for Experiment 1, volume of the dissected tracts was incorporated to the DWI tractography analysis. The results of the regression analysis for the SLF ($F(1,18) = 8.69$, $p = 0.003$, R^2

= 0.521) showed that the volume of the right SLF I and III were significant predictors for the TMS effects over response criterion (Beta'' index), $\beta = 0.376$, p = 0.047 and $\beta = -0.667$, p = 0.002, respectively (fig. 5A-B). When including the volume of the right SLF III as a covariate for the repeated-measures ANOVA for Beta'', the interaction between Region and Congruency reached significance, F(1, 17) =11.71, MSE = 0.095, p = 0.003, η^2p = 0.41, and this interaction depended on the volume of the right SLF III, F(1, 17) = 10.49, MSE = 0.095, p = 0.005, η^2p = 0.38. TMS over the right FEF (as compared with the vertex condition) was associated to a more liberal response criterion for incongruent Stroop trials. However, this effect was mainly observed in participants with low integrity values of the left FAT (see figure 5C-D). No significant interactions between region and congruency were found when the right SLF I was included as a covariate (all ps > 0.712). No other significant models were found for other tracts in any of the behavioral measures (all ps > 0.236).

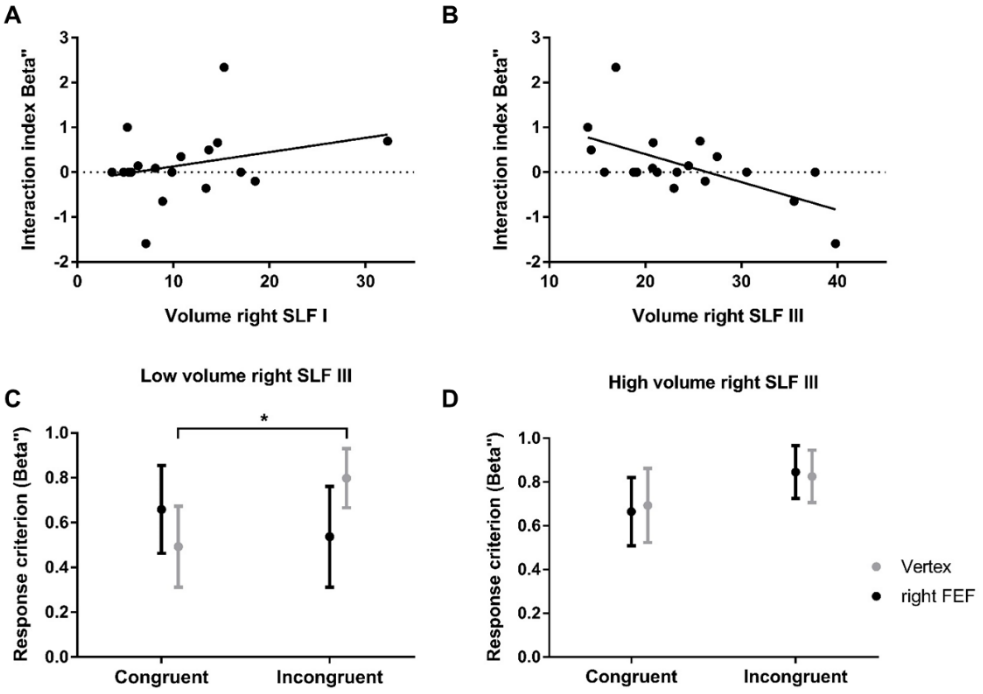

Figure 5. (**A, B**) Correlation between the volume (in ml) of the right SLF I and SLF III, and the FEF-TMS effect (Experiment 2) for response criterion. The black line represents the best fit of the data. (**C**, **D**) For experiment 2, Region and Congruency interaction for response criterion for participants with a volume of the right SLF III under the median (low volume) and over the median (high volume). Errors bars represent standard errors.

DISCUSSION

The aim of this work was to explore the involvement of a frontal region, the right SMA, in the interaction between executive control and conscious perception by using TMS, a methodology that allows establishing causal relations by temporally modulating the state of the brain. In a dual task, executive control was manipulated with a Stroop task in which congruent and incongruent trials were presented at the same time that a near-threshold Gabor stimulus had to be detected. This work aims to contribute to the current debate about the nature of the relation between conscious perception and attention, by exploring the executive control network, which in this context has been much less studied than other attentional networks. Also, this work aims to contribute to the debate about the involvement of the frontal regions and the fronto-parietal network in conscious perception. The right SMA (Experiment 1) and the right FEF (Experiment 2) were stimulated by using online TMS. Also, the implication of fronto-parietal white matter was explored thought the delineation of the three branches of the SLF. Complementarily to the preliminary hypothesis, the involvement of white-matter tracts connecting the targeted region (i.e. the SMA) with other relevant regions was explored through the delineation of the FAT and the SPL-SMA complex of the SLF I. A white matter macroscopic property of the tracts (i.e. volume) was also examined.

Behaviorally, in both Experiment 1 and 2, perceptual sensitivity to detect the near-threshold Gabor was significantly reduced for incongruent compared to congruent Stroop trials. However, no effects of executive control over decision criteria were found. In previous studies using a similar paradigm, executive control elicited by the Stroop task influenced participants' response criterion (Colás et al., 2018, 2017) or the percentage of seen targets (Martín-Signes et al., 2018) but not perceptual sensitivity. One difference between the present experiment and the ones listed above is the response modality employed for the Stroop task, which changed from a manual to a vocal-response. It has been well stablished that vocal-response interference excess manual-response interference (MacLeod, 1991; White, 1969). It has also been demonstrated that the size of the stimulus set can affect the evoked interference as exact stimulus repetition can produce priming effects (Hommel, 1998; Mayr, Awh, & Laurey, 2003). In the present experiment, we expanded the stimulus set by using four different word colors (compared with the three-color set used previously). The changes introduced in the paradigm (a vocal-response and a bigger set size) might have induced a greater interference effect that might account for the different results found. It is possible that a greater involvement of executive control mechanisms in the incongruent compared with the congruent trials is needed in order to modulate perceptual sensitivity to detect near-threshold stimuli.

In Experiment 1, TMS was applied over the right SMA or a control stimulation site (vertex) concurrently with the dual task. Previous fMRI work

(Martín-Signes et al., 2018) demonstrated that functional connectivity increased between the right SMA-SPL for congruent trials when near-threshold Gabors were reported as compared to non-reported Gabors. No differences in functional connectivity between these regions were observed on incongruent trials. Therefore, the TMS modulation of the SMA compared to the vertex condition was expected to produce differential effects over conscious perception depending on the executive control condition (i.e. congruent or incongruent). However, we did not find any SMA-TMS effects when exploring the contribution of executive control over perceptual sensitivity or response criterion.

A further aim of this work was to explore the contribution of long-range white matter tracts connecting the parietal and the frontal lobes in conscious access and its relation with executive control. Some studies have linked the microstructure of the SLF with different measures of the executive functions in healthy population (Crespi et al., 2018; Sasson et al., 2012, 2013; Smolker, Friedman, Hewitt, & Banich, 2018) and with executive dysfunctions in several conditions (Chiang et al., 2016; Makris et al., 2008; Muir et al., 2015; Oh, Shin, Choi, Lee, & Bang, 2018; Sui & Rajapakse, 2018; Wu et al., 2019). Some other studies have found a relation between the microstructure of the SLF and conscious perception or consciousness disorders (Bourgeois et al., 2015; Colás et al., 2019; Matthews, Spadoni, Lohr, Strigo, & Simmons, 2012; Matthews et al., 2011). However, literature exploring the contribution of the different dorsal-to-ventral branches of the SLF to executive control or conscious perception (or its interaction) is scarce (but see Colás et al., 2019; Quentin, Chanes, Vernet, & Valero-Cabré, 2014; Wu et al., 2019).

In addition, previous work has shown that neural interactions between different attentional networks and conscious perception are modulated by the microstructure of the SLF. Using functional MRI measures of the neural interaction between both processes, reduced integrity of the left SLF III was associated with a greater neural interaction between spatial orienting and conscious perception; while increased integrity of the left SLF III was associated with a greater neural interaction between phasic alerting and conscious perception (Chica et al., 2018). Moreover, reduced integrity of the left SLF II was associated with a greater neural interaction between executive control and conscious perception (Martín-Signes et al., 2018).

In accord, we performed linear regression analyses including the microstructure of the three branches of the SLF for the right and left hemispheres as predictors of the TMS modulation of the executive control and conscious perception interaction, reflected in perceptual sensitivity and response criterion. For Experiment 1, the results of the linear regression showed that the right SLF III was a significant predictor for the TMS effect on perceptual sensitivity (A’) and response criterion (Beta’’). When the microstructure of the right SLF III was included as a covariate in the ANOVA, results indicated that the TMS over the SMA reduced perceptual sensitivity (A’) only for the incongruent Stroop condition. As previously shown (Martín-Signes et al., 2017), participants with lower HMOA were the ones showing larger TMS effects. There is evidence in the literature that the SLF III participates in executive control and conscious perception and thus, it may be that a good integrity of this long-range fronto-parietal tract prevents from the disruption caused by the SMA stimulation and, only for participants with lower integrity of the tract, behavioral effects are observed.

Some studies have demonstrated a modulation of the stimulation-induced interference in the behavior, produced by the microstructural properties in the white matter tracts connecting the targeted region and other key regions in the involved circuits (Barredo et al., 2019; Brodie, Borich, & Boyd, 2014; Quentin, Chanes, Migliaccio, Valabrègue, & Valero-Cabré, 2013; Quentin et al., 2014; Rodríguez-Herreros et al., 2015). In our study, only the SLF I innervates the SMA, while the SLF II and III do not (Vergani et al., 2014). However, the SLF III connects (among other structures) the inferior frontal gyrus (IFG), which participates in cognitive control and is well connected with the SMA through the FAT (Nakajima et al., 2019; Vergani et al., 2014). Thus, it is also plausible that a well-connected SMA-IFG by the SLF III prevents from the disruptive effects of TMS over the SMA. Indeed, the microstructure of the left FAT was a significant predictor for the SMA-TMS effects over perceptual sensitivity and response criterion. In line with the results obtained for the SLF III, participants with lower integrity of this tract showed greater TMS effects over perceptual sensitivity. As mentioned, the FAT originates in the SMA complex and terminates in the IFG, which is also the termination of the SLF III. Although the definition of this tract is recent (Catani et al., 2012), it has been proposed a role on control, planning and coordination of motor programs and the inhibition of competing motor plans. Some level of hemispheric specialization has been found, with a left FAT particularly involved in speech actions and a right FAT more related with inhibitory control, especially in the visuo-spatial domain (Dick et al., 2019). Although an involvement of the right FAT was expected because of the hemispheric location of the stimulated SMA and the right SLF III association found, the verbal nature of the Stroop task employed could account for the observed results. Also, the microstructure of the right SPL-SMA complex of the SLF I was a significant predictor for the SMA-TMS effects over response criterion. This result is in agreement with a previous study in which functional connectivity between the right SMA and the right SPL reflected an interaction between executive control and conscious perception (Martín-Signes et al., 2018). Nevertheless, due to the post hoc nature of these analysis, they should be interpreted with caution.

In Experiment 2, the right FEF was selected as an active control region to demonstrate that the TMS effects found over the right SMA were region specific. In a previous study (Martín-Signes et al., 2018), larger BOLD responses were found for seen than unseen trials on the right FEF, and thus, an effect was expected for conscious perception but not for executive control or for the interaction between both processes. Nevertheless, we did not find a TMS effect over consciousness (neither a modulation related to the microstructure of the SLF). This result is in agreement with theories arguing that consciousness is a distributed process and does not rely in a specific region (Dehaene & Changeux, 2011) and thus, the modulation of one particular region may not be enough to impair conscious perception. Conversely, a main TMS effect over executive control was found, as TMS over the right FEF increased Stroop accuracy compared with the vertex condition. Although this result was unexpected, there are examples in the literature showing a role of FEF in attentional control (Cosman, Lowe, Woodman, & Schall, 2018; Muggleton, Juan, Cowey, & Walsh, 2003) and inhibitory control (Muggleton, Chen, Tzeng, Hung, & Juan, 2010; Xu et al., 2007), both processes presumably involved in resolving the Stroop task.

The post hoc exploration of the macroscopic properties of the tracts showed that TMS over the right FEF modulated response criterion on incongruent trials when the volume of the right SLF III was taken into account. The convergence of results over this tract in Experiment 1 and 2, and in previous work (Colás et al., 2019; Martín-Signes et al., 2017), suggest a role of the right SLF III on conscious perception and its relation with some attentional processes, such as executive control, and phasic alerting. Nevertheless, further investigation is needed to better understand the relation between micro- and macroscopic properties of the tracts and behavioral or TMS-related variables.

Although interesting, the findings of this work need to be understood in the context of some limitations, some of them intrinsic to many TMS designs. One important point is that the SMA complex is a medial structure and the TMS pulse might not reach deeper layers. It is plausible that the partially null results of this work (when white matter properties are not taken into account in the analyses) are due to a difficulty on the stimulation of the SMA. Also, the TMS targets for this investigation were situated over the right hemisphere. Although DWI data were extracted from tract from both hemispheres, further investigation from left targets and networks is needed. Finally, correlations between DWI tractography and behavioral measures were explored with a limited number of participants. Also, post hoc examinations increased the number of comparisons. Further studies with larger samples and *a priori* hypothesis would allow to confirm the findings.

To conclude, the results of this work can be summarized in some key contributions. They support the behavioral interaction between executive control and conscious perception, showing that a greater interference is needed to observe a modulation of perceptual sensitivity. However, although the investigation of the neural interactions between executive control and conscious perception has produced positive results (Colás et al., 2018; Martín-Signes et al., 2018 and the present study), it seems to be less robust than the interaction found between consciousness and other attentional systems (namely spatial attention, Chica et al., 2010, 2013; Chica, Valero-Cabré, Paz-Alonso, & Bartolomeo, 2014; Rees & Lavie, 2001, and alerting, Chica et al., 2016, 2018; Cobos, Guerra, Vila, & Chica, 2019). It is plausible that the overlap between regions or neural mechanisms involved in executive control and conscious perception is less massive, resulting in a less consistent neural and behavioral interaction. In the present study, the neuromodulation of a frontal region, the right SMA, only affected perceptual sensitivity on incongruent trials when the integrity of the right SLF III or the left FAT were introduced in the analysis. Similarly, the stimulation of the right FEF only affected the response criterion on incongruent trials when the volume of the right SLF III was taken into account. Nevertheless, these findings do not rule out the implication of frontal regions in conscious perception and point to fronto-parietal and frontal networks as the possible shared neural substrates between both systems. Finally, the TMS-effects dependence on the micro- and macrostructure of some fronto-parietal and frontal tracts suggest that white matter properties might be taken into account as a source of individual variability and efficiency in TMS studies. While a direct implication of white matter tracts connecting the neuromodulated regions have been shown before (Barredo et al., 2019; Brodie et al., 2014; Quentin et al., 2013, 2014; Rodríguez-Herreros et al., 2015), these results (and others before, Martín-Signes et al., 2017) suggest that an indirect modulation thought compensatory processes supported by different anatomical networks is also plausible.

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OPEN PRACTICES

Materials and data for the study are available at https://osf.io/g8ue5/?view_only=b54ba6ec57b54810b92a220f402da6e8. The conditions of our ethics approval do not permit public archiving or sharing of anonymized raw study data. We report sample size calculations, 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. No part of the study procedures and analyses were pre-registered prior to the research being conducted.

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