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Title: Modulating the influence of recent trial history on attentional capture via transcranial magnetic stimulation (TMS) of right TPJ

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Abstract

In visual search, salient yet task-irrelevant distractors in the stimulus array interfere with target selection. This is due to the unwanted shift of attention towards the salient stimulus—the so-called attentional capture effect, which delays deployment of attention onto the target. Although powerful and automatic, attentional capture by a salient distractor is nonetheless antagonized by distractor-filtering mechanisms and is further modulated by cross-trial contingencies: The distractor cost is typically more robust when no distraction has been experienced in the immediate past, compared to when a distractor was present on the immediately preceding trial. Here, we used transcranial magnetic stimulation (TMS) to shed light on the causal role of two crucial nodes of the ventral attention network, namely the Temporo-Parietal Junction (TPJ) and the Middle Frontal Gyrus (MFG), in the exogenous control of attention (i.e., attentional capture) and its history-dependent modulation. Participants were asked to discriminate the direction of a target arrow while ignoring a task-irrelevant salient distractor, when present. Immediately after display onset, 10 Hz triple-pulse TMS was delivered either to TPJ or MFG on the right hemisphere. Results demonstrated that stimulation of right TPJ—but not of right MFG, strongly modulated attentional capture as a function of the type of previous trial, by somewhat enhancing the distractor-related cost when the preceding trial was a distractor-absent trial and significantly decreasing the cost when the preceding trial was a distractor-present trial. These findings indicate that TMS of right TPJ exacerbates the effect of the recent history, likely reflecting enhanced updating of the predictive model that dynamically governs proactive distractor-filtering mechanisms. More generally, the results attest to a role of TPJ in mediating the history-dependent modulation of attentional capture.

Keywords: Transcranial magnetic stimulation; Attentional capture; Temporo-parietal junction; Middle-frontal gyrus; Ventral attentional network

1. Introduction

The ability to interact successfully with our rich visual environment depends on sophisticated and flexible visual selective attention mechanisms, which allow selecting relevant information while disregarding irrelevant stimuli (Chelazzi, Marini, Pascucci, & Turatto, 2019, 2011; Desimone & Duncan, 1995; Forster & Lavie, 2008; Jonides & Yantis, 1988; Marini, Chelazzi, & Maravita, 2013; Reynolds & Chelazzi, 2004; Yantis & Jonides, 1990). Salient, attention-grabbing stimuli involuntarily capture the participant's attention, interfering with the ongoing task, although a panoply of distractor-filtering mechanisms exist that try and counteract such unwanted capture of attention (for a review, see Chelazzi et al., 2019; Geng, Won, & Carlisle, 2019).

Distractor-filtering mechanisms may intervene proactively via top-down control whenever potential distraction is foreseen in order to limit the likely performance cost from distracting stimuli (i.e., before they are actually presented). Besides guidance via higher-level cognitive control, distraction-filtering may be the result of the engagement of lower-level and possibly automatic mechanisms. Indeed, attentional capture is known to be modulated by repeated exposure to a certain distractor (e.g., habituation of capture, see Neo & Chua, 2006; Pascucci & Turatto, 2015, Turatto, Bonetti, & Pascucci, 2017, 2018), as well as by the implicit manipulation of the spatial probability distribution of (targets and) distractors (Di Caro, Theeuwes, & Della Libera, 2019; Ferrante et al., 2018; Goschy, Bakos, Muller, & Zehetleitner, 2014; Sauter, Liesefeld, & Müller, 2019, 2018; Wang & Theeuwes, 2018b, 2018a) and by inter-trial priming (Geyer, Müller, & Krummenacher, 2008; Goschy et al., 2014; Müller et al., 2010).

Inter-trial contingency effects refer to the facilitation of distractor filtering if the distractor was present (versus absent) in the preceding, n-1 trial. Although the influence of inter-trial contingencies is a well-established phenomenon, the underlying mechanisms are not fully understood (Chelazzi et al., 2019). Likely, this facilitation is due to the fact that distractor-filtering mechanisms remain in a state of persistent activation (Marini et al., 2013, 2016). This is also in line with the observation that the influence of inter-trial contingencies is modulated by the context, decreasing with increasing overall distractor frequency across the experimental session. In particular, greater inter-trial effects have been observed under low overall distractor probability (i.e., when sustained proactive filtering mechanisms are less likely recruited), whereas a less consistent effect or no effect has been observed under higher distractor probability (i.e., when tonic proactive mechanism are active) (Geyer et al., 2008; Müller, Geyer, Zehetleitner, & Krummenacher, 2009).

The neural mechanisms that the brain can implement to limit or counteract distraction by salient, unexpected stimuli have received mounting interest in the recent years (Chelazzi et al., 2019; Geng, 2014; Geng et al., 2019). Numerous functional imaging studies demonstrated that attentional control in the presence of potential salient distraction is linked to the activation of the dorsal frontoparietal attention network, whose core regions include the frontal eye field (FEF) and the posterior parietal cortex, including tissue within the intraparietal sulcus (IPS), and the ventral frontoparietal network, whose core regions include the temporo-parietal junction (TPJ) and the middle-inferior frontal gyrus (IFG and MFG) (Corbetta & Shulman, 2002; de Fockert, Rees, Frith, & Lavie, 2004; de Fockert & Theeuwes, 2012; DiQuattro, Sawaki, & Geng, 2014; Leber, 2010; Lee & Geng, 2017; Marini, Demeter, Roberts, Chelazzi, & Woldorff, 2016; Melloni, Van Leeuwen, Alink, & Müller, 2012; Serences, Yantis, Culberson, & Awh, 2004, 2005; Talsma, Coe, Munoz, & Theeuwes, 2009). However, an inherent limitation of neuroimaging studies is the inability to reveal any causal organization in the described relationships between brain activity and behavioral performance. Furthermore, functional neuroimaging lacks the temporal resolution to establish whether and how each element of the network is causally involved in determining attentional capture and supporting any distractor filtering mechanism.

In a recent study (Lega et al., 2019), a systematic transcranial magnetic stimulation (TMS) approach was adopted to comparatively assess the causal role of both FEF and IPS in the dorsal attention network on either side of the brain. A substantial reduction of the distractor cost emerged following rTMS of right (but not left) FEF. This result suggested that the stimulation of the right FEF improved distractor suppression mechanisms by activating neural circuits involved in attentional regulation, therefore allowing for more successful inhibition of task-irrelevant information. Interestingly, right FEF stimulation also affected history-contingent modulation of attentional capture, by entirely eliminating the relative (extra) cost in performance when a distractor-present trial was preceded by a distractor-absent trial (of note, the latter result was similarly obtained by stimulating right IPS). Stimulation of right FEF thus seemed to be able to mimic the effect of having encountered a distractor on the preceding trial, perhaps by priming dedicated mechanisms for the filtering-out of distractors, when actually encountered.

Altogether, these findings demonstrated that it is possible to ignite cortical mechanisms that are responsible for distractor suppression by means of TMS. In the present study, we extended the investigation of putative mechanisms for distractor-filtering to the ventral attention network, by targeting two regions that are often involved in attentional processing, including distractor suppression, namely the TPJ and the MFG in the right hemisphere. The right MFG has been demonstrated to be a pivotal hub for proactively filtering distracting information and its activation correlates with behavioral indexes of distractor suppression (Demeter, Hernandez-Garcia, Sarter, & Lustig, 2011; Marini et al., 2016; Weissman, Roberts, Visscher, & Woldorff, 2006). Furthermore, neuropsychological evidence indicated the rMFG as a crucial node for regulating both top-down and bottom-up attention (see Japee, Holiday, Satyshur, Mukai, & Ungerleider, 2015). Congruently, resting-state analysis suggested that part of the ventrolateral frontal cortex, and specifically the right MFG, may link dorsal and ventral attention networks (Fox, Corbetta, Snyder, Vincent, & Raichle, 2006; He et al., 2007). Together with the right MFG, the right TPJ is traditionally considered to be a critical part of a right-lateralized ventral attentional network that re-orient attention toward the appearance of unexpected, but behaviorally relevant events in the environment (Corbetta, Patel, & Shulman, 2008; Corbetta & Shulman, 2002; Downar et al., 2002; Dugué, Merriam, Heeger, & Carrasco, 2018; Shomstein et al., 2012). Evidence for a role of right TPJ in attentional re-orienting came principally from studies using variants of the Posner task, where TPJ activation occurred predominantly in response to invalidly cued targets (i.e., when attentional re-orienting is required) (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Doricchi, Macci, Silvetti, & Macaluso, 2010; Indovina & Macaluso, 2007; Kincade, 2005; Natale, Marzi, & Macaluso, 2010; Vossel, Thiel, & Fink, 2006). However, more recent evidence suggested that TPJ activation may not be specific for stimulus-driven attentional re-orienting, but may instead reflect post-perceptual processes involved in contextual updating and adjustments of top-down expectations (DiQuattro et al., 2014; Geng & Vossel, 2013; Han & Marois, 2014; Mengotti, Dombert, Fink, & Vossel, 2017; Vossel, Mathys, Stephan, & Friston, 2015).

Building on these premises, the purpose of this study was twofold. First, we aimed at investigating the causal role of the right ventral attention network (TPJ and MFG) in the mechanisms involved in attentional capture and the filtering of salient but irrelevant distractors. Second, based on previous findings that established a role of the ventral attention network in proactive attentional processes and the contextual updating of predictive models, we tested the role of TPJ and MFG by means of TMS in the regulation of cross-trial dynamics of distractor-filtering.

2. Materials and methods

All relevant methodological details of the present study are reported in what follows, including how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analyses, all manipulations, and all variables measured in the study. No part of the study procedures, nor of the study analyses was pre-registered prior to the research being conducted. The datasets, the digital study materials and the analysis codes generated during the current study are available online at <https://osf.io/nry9v/>, stored on the Open Science Framework data sharing platform.

2.1. Participants

Sample size was determined on the basis of one previous study from our lab (Lega et al., 2019) wherein the same behavioral paradigm and a similar TMS protocol were implemented (see below). Inclusion criteria for participants were established prior to the experiment, including normal vision, right-handedness, an age between 18 and 35 years, and no contraindications for TMS use, as detailed in what follows; moreover, individual participants' data would have not been included in the final dataset unless the experimental session was completed (and therefore an adequate number of repetitions of each experimental condition

was available). Thirty-one healthy volunteers took part in the experiment (24 F; mean age = 23.61, SD = 3.32). One participant had to be excluded due to a technical problem. Therefore, data from thirty participants (23 F, mean age = 23.67, SD = 3.33) were used for the analyses reported below. All participants were right-handed and with normal or corrected-to-normal visual acuity and normal color vision. Prior to the TMS experiment, each subject filled-in a questionnaire to evaluate eligibility for TMS. None of the participants reported any contraindications for TMS use (Rossi, Hallett, Rossini, & Pascual-Leone, 2009). Written informed consent was obtained from all participants prior to the beginning of the experiment. The study protocol was approved by the local ethical committee and the experiment was conducted in accordance with the Declaration of Helsinki.

2.2. Stimuli

A version of the paradigm similar to the one used in the current experiment has been used before in our lab (Ferrante et al., 2018; Lega et al., 2019). The visual search display consisted of four stimuli (one per visual quadrant) presented equidistantly from one another and centered around a central fixation point (eccentricity: 4°). All stimuli were composed of two green or red triangles (1° × 1° each; green: RGB 0, 104, 0; luminance 31.1 cd/m²; red: RGB 216, 0, 0; luminance 31.8 cd/m²) presented on a light grey background (RGB 167, 167, 167; luminance 95.9 cd/m²). In half of the trials, all display items were of the same color (e.g., red; distractor-absent condition), whereas in the other half, three items were of the same color (e.g., red) and the remaining item (additional singleton) was of the alternative color (e.g., green; distractor-present condition). The target was defined as the only item in the display with both triangles pointing in the same direction (both up or both down, i.e., a double arrow-head), whereas the singleton distractor, when present, was a color-singleton stimulus with both triangles pointing outwardly. The remaining stimuli (non-targets or fillers) were always of the same color as the target and with both triangles pointing inwards.

2.3. Procedure

Participants were seated in front of a 17" CRT monitor (spatial resolution of 1280 × 1024-pixel and a refresh rate of 75 Hz) at a distance of 57 cm, in a dimly illuminated, silent room. A chin rest was used to keep the viewing distance constant during the whole session. Each trial began with a fixation point displayed in isolation for 1000 ms, followed by an array of four placeholders, which were identical to non-targets, and were presented for 700 ms (Fig. 1A). At the end of the 700-ms period, one of the placeholders was replaced by the target and, on half of the trials, a different placeholder was replaced by the singleton distractor (Ferrante et al., 2018; Lega et al., 2019).

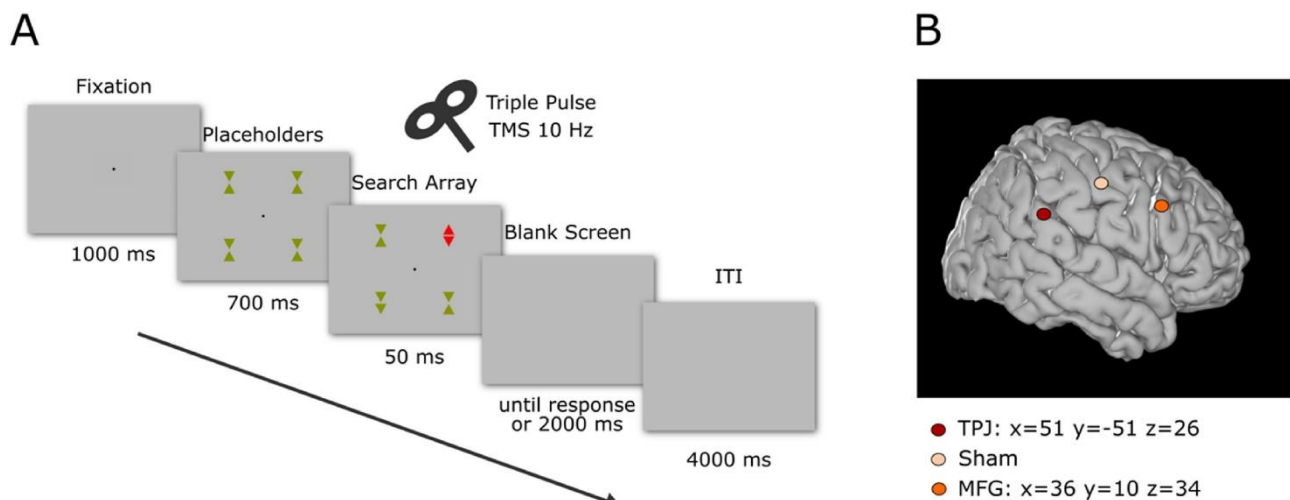


Fig. 1. Experimental procedure. (A) Timeline of an experimental trial: After 1000 ms of fixation display, the placeholder screen was shown for 700 ms. The search array was then presented for 50 ms, after which a

blank screen was displayed. Participants had a maximum of 2000 ms from the onset of the search array to indicate the orientation of the target. A new trial started after 4000 ms. Three TMS pulses were delivered at 10 Hz (pulse gap of 100 ms) starting 100 ms after search array onset. (B) Talairach coordinates of the right TPJ: $x = 51$, $y = -51$, $z = 26$ and the right MFG: $x = 36$, $y = 10$, $z = 34$ visualized in the probabilistic JuBrain-Cytoarchitectonic-Atlas-Viewer (Mohlberg, Eickhoff, Schleicher, Zilles, & Amunts, 2012). The sham condition was delivered in a region on the scalp located halfway between TPJ and MFG of the right hemisphere.

This array remained visible for 50 ms and was followed by a blank screen, which lasted until the participant responded or 2000 ms had elapsed, whichever came first. Trials were separated by a 4000-ms inter-trial interval (Fig. 1A). Participants were instructed to indicate as quickly and as accurately as possible whether the target element was pointing up or down by pressing '1' for 'up' or '2' for 'down' on a numeric keypad. Key assignments were counterbalanced across participants. Before the experiment, participants completed a practice block of 24 trials to familiarize with the task, followed by 6 experimental blocks (two per each of the three TMS conditions, see below). Each block consisted of 96 trials, 48 of which were distractor-present and 48 distractor-absent. Within each block, the target and the singleton distractor were presented equally often at any given spatial location. The order of the TMS blocks had an A-B-C-A-B-C structure, in which A, B and C stand for the three stimulation sites (Sham, TPJ, and MFG; see below), and was randomized across participants in order to spread out any potential learning effect equally across TMS conditions. The entire experiment lasted approximately 2.5 h. The software Open-Sesame (Mathôt, Schreij, & Theeuwes, 2012) was used for stimulus presentation, data collection and TMS triggering.

2.4. Transcranial magnetic stimulation (TMS)

Online neuronavigated TMS was delivered using a Magstim Rapid2 stimulator (Magstim Co Ltd, Whitland, UK) connected to a 70-mm butterfly coil. Targeted sites were the right Temporo-Parietal Junction (TPJ) and the right Middle Frontal Gyrus (MFG). We identified a suitable sham condition in a region on the scalp located between TPJ and MFG. The two active TMS sites were localized by means of stereotaxic navigation on individual estimated magnetic resonance images (MRI) obtained through a 3D warping procedure fitting a high-resolution MRI template with the participant's scalp model and craniometric points (Softaxic, EMS, Bologna, Italy). This procedure has been proven to ensure a global localization accuracy of roughly 5 mm, a level of precision close to that obtained using individual MRIs (Carducci & Brusco, 2012). The targets in individual brains were identified by means of Talairach coordinates on the standard MRI template and then warped to fit the subject's skull. The mean, representative coordinates were extrapolated from the previous imaging literature. Right TPJ coordinates were $x = 51$, $y = -51$, $z = 26$ and were extracted from the averaged Talairach (Talairach & Tournoux, 1988, p. 132) coordinates of prior fMRI (Kincade, 2005) and TMS (Bourgeois, Chica, Valero-Cabré, & Bartolomeo, 2013a; Chica, Bartolomeo, & Valero-Cabre, 2011) studies (Fig. 1B). MFG Talairach coordinates ($x = 36$, $y = 10$, $z = 34$; Fig. 1B) were obtained by converting the MNI coordinates of the site of interest from a neuroimaging study which focused on the neural circuits of proactive and reactive mechanisms for filtering distracting information (Marini et al., 2016).

The resting motor threshold (rMT) was determined using a software-based "adaptive method" developed by Awiszus (2003) (Motor Threshold Assessment Tool, MTAT, version 2.0: <http://www.clinicalresearcher.org/software.htm>). Any visible muscle twitch was entered in the software as a "valid response". During the experiment, TMS was delivered at 100% of the individual rMT (mean intensity = 51% of the maximum stimulator output). For all participants, the TMS intensity was kept constant for both TPJ and MFG stimulation. For the right MFG, the coil was initially oriented with an angle of approximately 45° from the nasion-inion line and the handle pointing outwards, and then slightly adjusted (around $\pm 3-4^\circ$) for each participant in order to minimize discomfort. For right TPJ, the coil was held tangential to the scalp, with the handle pointing backward. Finally, for the sham condition, the coil was

held perpendicular to the scalp in order to ensure that the magnetic field did not stimulate the underlying cortex: This sham condition has been proven to be ineffective in producing an electric field capable of changing neuronal excitability (Lisanby, Gutman, Luber, Schroeder, & Sackeim, 2001). Three TMS pulses were delivered at 10 Hz (pulse gap of 100 ms) starting 100 ms after search array onset (see Fig. 1). Triple-pulse 10 Hz TMS starting at 100 ms covered a time-window (100–300 ms) that is critical for attentional capture effects and distractor suppression mechanisms, as shown by human scalp electrophysiology (Jannati, Gaspar, & McDonald, 2013; H. R.; Liesefeld, Liesefeld, Töllner, & Müller, 2017; McDonald, Green, Jannati, & Di Lollo, 2013). Furthermore, the same TMS protocol has proven effective before in modulating distractor filtering mechanisms (Lega et al., 2019).

2.5. Statistical analysis

The statistical approach implemented here is the same as that used and described in Lega et al., 2019. Specifically, reaction times (RTs) were log-transformed prior to the analysis in order to assuage deviations from normality (before transformation: skewness = 1.97, kurtosis = 5.86; after transformation: skewness = .18, kurtosis = -.06). Only correct-response trials were included in the RT analysis (a total of 5.8% of trials were excluded). Linear mixed-effect models were used as the main statistical procedure (Baayen, Davidson, & Bates, 2008). We set up each model following Barr, Levy, Scheepers, and Tily's (2013) recommendation to model the maximal random-effects structure justified by the experimental design. Statistical significance was tested with the F-test with Satterthwaite approximation of degrees of freedom. All the models were estimated using R (R Development Core Team, 2016) and the lme4 package (version 1.1–12) (Bates, Maechler, Bolker, & Walker, 2014). In addition to the RT analysis, we conducted an accuracy analysis on all conditions; however, since no significant effect of TMS emerged from the accuracy analysis, we will not report those results. Bayesian analysis were performed using JASP software (<https://jasp-stats.org/>). Finally, raincloud plots were used for illustration of the data (Allen, Poggiali, Whitaker, Marshall, & Kievit, 2019).

3. Results

3.1. Effect of TMS: on-line effects on visual search performance

We tested the effect of TMS on attentional capture and distractor filtering mechanisms using a linear mixed model that predicted log-transformed RTs of correct-response trials. The experimental factors TMS (sham vs. MFG vs. TPJ), Distractor presence (present vs. absent) and their interaction were included as fixed effects. Random coefficients across participants were estimated for intercept and for the factors TMS and distractor presence. The analysis revealed a significant main effect of Distractor presence, $F(1, 28.8) = 214.49$, $p < .001$, indicating that participants were overall faster in the distractor-absent condition ($M = 375$ ms, $SD = 229$ ms) compared to the distractor-present condition ($M = 467$ ms, $SD = 257$ ms), with an average distractor cost of 92 ms. The main effect of TMS was not significant, $F(2, 29) < 1$, $p = .77$. The interaction between Distractor presence and TMS was not significant, $F(2, 16234) < 1$, $p = .80$, indicating that overall TMS did not significantly interact with the cost of distraction (Fig. 2). In order to assess the extent to which the data support the presence and, respectively, the absence of the above effects, we also performed a Bayesian analysis. Bayesian ANOVA indicated that all models (except TMS) receive overwhelming evidence in comparison to the Null model. The model that outperforms the Null model the most is the main effect model that only includes Distractor presence as predictor. Adding the interaction makes the model less competitive. The evidence against including the interaction is roughly a factor of 106 ($BF_{10}(\text{Distractor presence}) = 1234e+33$)/ $BF_{10}(\text{TMS} \times \text{Distractor presence}) = 1160e+31$, indicating that the data are 106 times more likely under the main effect of Distractor presence model than under the model that adds the interaction TMS x Distractor presence.

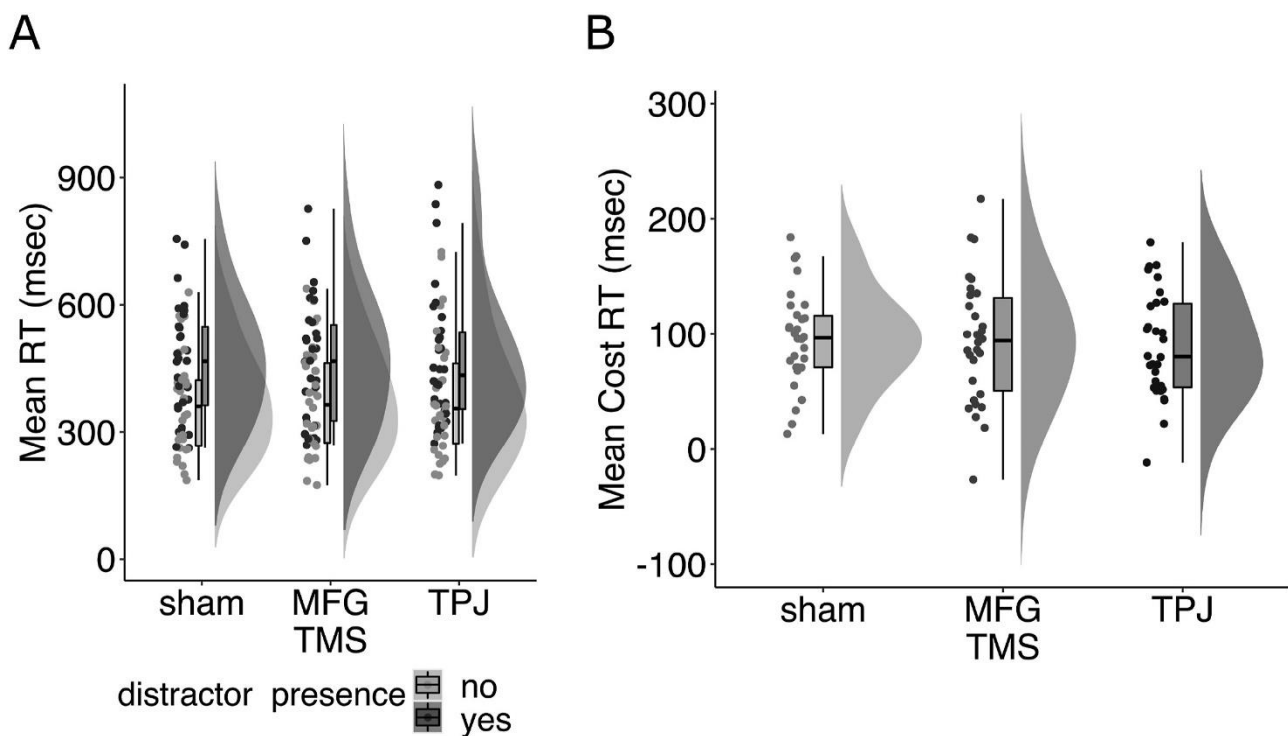


Fig. 2. TMS effects on on-line visual search performance. (A) Mean RTs for the distractor-present condition and distractor-absent condition and (B) Mean RT cost (difference RTs for trials in which there was a singleton distractor relative to trials in which it was absent) shown for each participant (indicated by individual points) together with boxplots and sample density, as a function of TMS site (sham vs. MFG vs. TPJ).

In order to verify whether the TMS effect depends on the spatial position of the distractor and/or of the target in the given search display, we analyzed RTs in the distractor-present condition as a function of whether the target and distractor appeared in the right or left visual field, i.e., ipsilateral or contralateral to the stimulation. Therefore, we implemented a linear mixed model with the experimental factors TMS (sham vs. MFG vs. TPJ), Target side (right vs. left) and Distractor side (right vs. left) as fixed effects. The random effect structure included the random intercept for subject, as well as the by-subject random slope for TMS, Target side and Distractor side. As expected, the analysis indicated a significant interaction between Target side and Distractor side, $F(1, 7969.6) = 26.63$, $p < .001$, reflecting longer RTs when target and distractor were on the same side ($M = 480$ ms, $SD = 257$ ms) compared to opposite sides ($M = 462$ ms, $SD = 256$ ms). This is in line with previous studies, demonstrating a bilateral field advantage (BFA) in early visual attentional processing, i.e., enhanced visual processing when (relevant) stimuli are spread across both visual hemifields (Alvarez & Cavanagh, 2005; Kraft et al., 2005; Lega et al., 2019; Sereno & Kosslyn, 1991). However, TMS did not interact with either Target side, $F(2, 7971.9) < 1$, $p = .39$, or Distractor side $F(2, 7970.0) = 1.82$, $p = .16$, or their interaction $F(2, 7967.2) = 1.10$, $p = .33$.

3.2. Effect of TMS: modulation of cross-trial contingencies

Assuming that a given visual search paradigm is effective in eliciting robust distractor interference, consistent evidence also demonstrated that this interference is typically attenuated when the preceding trial contains a distractor (Chelazzi et al., 2019; Geyer et al., 2008; Goschy et al., 2014; Lega et al., 2019; Müller et al., 2009). Importantly, this effect is in turn dependent on the overall distractor frequency across the experimental session, with a greater effect being found under low distractor probability (i.e., 20%) and

a smaller or no effect under higher distractor probability (i.e., 50% or 80%) (see Geyer et al., 2008; Müller et al., 2009). In this analysis, we evaluated whether, and to what degree, TMS modulated history-dependent changes in the distractor costs, i.e., depending on the presence vs. absence of a distractor on the immediately preceding trial. To this aim, log-transformed RTs were predicted within a mixed linear model that included TMS (sham vs. MFG vs. TPJ), Distractor presence (present vs. absent) and Type of previous trial (distractor-present vs. distractor-absent) as fixed-effect factors and intercept, TMS, Distractor presence and Type of previous trial as random-effect coefficients across participants. A significant main effect of Distractor presence emerged, $F(1, 28.8) = 217.54$, $p < .001$, as in the previous analysis. Crucially, the three-way interaction TMS by Distractor presence by Type of previous trial was significant, $F(2, 16057) = 4.42$, $p = .011$. Contrast analysis showed that the distractor cost when the previous trial was a distractor-absent trial relative to a distractor-present trial significantly differed when comparing sham vs. TPJ conditions, $t = 2.70$, $p = .006$ ($b = -.08$, 95% CI = $[-.14; -.02]$), but not when comparing sham vs. MFG conditions, $t < 1$, $p = .78$ ($b = -.008$, 95% CI = $[-.07; .052]$). This effect reflected an increase in the distractor cost due to TPJ stimulation, following a distractor-absent trial (mean cost sham: 89 ms; mean cost TPJ: 106 ms) and, even more evidently, a marked decrease in the distractor cost due to the same stimulation following a distractor-present trial (mean cost sham: 100 ms; mean cost TPJ: 74 ms). A follow-up analysis showed that a similar contrast comparing TPJ and MFG stimulations was also significant, $t = 2.42$, $p = .016$, ($b = .07$, 95% CI = $[.01; .13]$), see Fig. 3. Raw RTs data as a function of distractor presence, TMS and the type of previous trial are shown in Table 1.

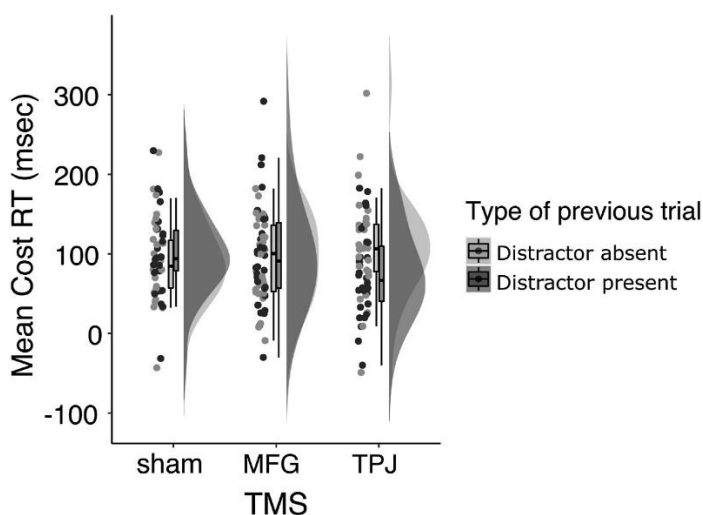


Fig. 3. Mean RT distractor cost shown for each participant (indicated by individual points) together with boxplots and sample density, as a function of TMS site (sham vs. MFG vs. TPJ) and the type of previous trial (Distractor-absent vs. Distractor-present condition). The difference in the distractor cost when the type of previous trial was a distractor-absent vs. a distractor-present condition was significantly different between both TPJ vs. sham, and TPJ vs. MFG. When the type of previous trial was a distractor-absent condition, TPJ stimulation relatively increased the distractor cost compared to the sham stimulation. When the type of previous trial was a distractor-present condition, TPJ stimulation significantly decreased the distractor cost compared to the sham stimulation.

In order to further explore this significant interaction, we conducted separate analyses based on the Type of previous trial (distractor-absent versus distractor-present). When a distractor was absent in the previous trial, no significant effect of TMS on the distractor cost was found, TMS by Distractor presence: $F(2, 7982.7) = 1.38$, $p = .25$. Conversely, when a distractor was present in the previous trial, TMS significantly modulated

the cost of distraction, $F(2, 8004.6) = 3.22$, $p = .039$. Contrast analysis demonstrated that when the type of trial was a distractor-present condition, the cost of distraction was significantly reduced after TPJ stimulation, $t = 2.33$, $p = .019$ ($b = -.05$, 95% CI = $[-.09; -.008]$), but not after MFG stimulation $t < 1$, $p = .76$ ($b = -.006$, 95% CI = $[-.04; .03]$), compared to the sham.

	Previous trial: absent		Previous trial: present	
	Distractor present	Distractor absent	Distractor present	Distractor absent
Sham	459 (241)	370 (223)	466 (254)	366 (211)
MFG	464 (246)	368 (217)	474 (265)	378 (225)
TPJ	477 (265)	371 (235)	463 (261)	389 (249)

Table 1. Mean RTs and standard deviation for each TMS condition as a function of distractor presence and the type of previous trial.

4. Discussion

This study sought to ascertain the causal role of two key regions of the right ventral attention network, MFG and TPJ, in modulating attentional capture elicited by salient distracting stimuli and its history-contingent modulation. Results indicated that stimulation of neither site produced measurable effects in the overall ability to filter-out salient distractors, unlike what we found by stimulating rFEF in our prior study (Lega et al., 2019). However, robust effects were found when considering modulations of the distractor cost provoked by recent trial history. More specifically, TMS of rTPJ, but not of rMFG, engendered an exacerbated manifestation of cross-trial dependency of performance. In particular, the distractor cost on the current trial was moderately (and non-significantly) magnified under rTPJ stimulation when the type of previous trial was a distractor-absent trial and robustly and significantly minimized when the type of previous trial was a distractor-present trial. This indicates that TMS of rTPJ enhanced the impact on performance of recent trial history, perhaps by boosting a mechanism for the rapid updating of an internal model based on evidence gathered through recent events, therefore rendering the system especially sensitive to the last episode along the trial sequence. This interpretation is consistent with the role of TPJ in contextual updating mechanisms, by evaluating and integrating ongoing stimulus information with internal expectations.

Previous findings indicated that within a stimulus presentation sequence, the distractor cost on the current trial tends to be smaller when preceded by a distractor-present compared to a distractor-absent condition (Geyer et al., 2008; Goschy et al., 2014; Lega et al., 2019; Müller et al., 2009). However, this inter-trial facilitation of distractor filtering also depends on the overall frequency of occurrence of the salient distractor over the course of the entire experiment. In particular, such history-dependent modulation tends to be stronger under conditions of relatively low distractor frequency during the session, compared to when the distractor appears more often (Chelazzi et al., 2019; Geyer et al., 2008; Marini et al., 2013; Müller et al., 2009). This is generally accounted for by assuming that, under conditions of high distractor frequency, the filtering-out of the salient distractor is predominantly accomplished by engaging a tonic proactive mechanism for distractor filtering, rendering inter-trial effects less impactful on performance (Chelazzi et al., 2019; Marini et al., 2013, 2016). In line with this notion, it is not uncommon that history-dependent modulations of the distractor cost are modest, if not absent altogether, with intermediate frequencies of distractor occurrence (e.g., 50%), as was the case in our paradigm (Geyer et al., 2008; Müller et al., 2009). In fact, in the sham control condition we did not observe a reliable inter-trial effect. However, rTPJ stimulation exacerbated the effect of the recent history, therefore revealing the causal role of right TPJ in fast inter-trial contextual adjustments.

This result aligns nicely with the “contextual updating” hypothesis (Geng & Vossel, 2013), postulating that right TPJ is a crucial node for updating internal models of the current behavioral context to the aim of optimizing effective decisions and responses (Chambon et al., 2017; DiQuattro & Geng, 2011; DiQuattro et al., 2014; Han & Marois, 2014; Mengotti et al., 2017; Vossel et al., 2015; for a review, see; Geng & Vossel, 2013). In this framework, we can hypothesize that the stimulation of right TPJ enhanced internal predictions over incoming trial-by-trial sensory evidence, hence preparing the system for dealing with salient and potentially task-irrelevant stimuli, although such strong dependence on recent trial history was not always beneficial to effective attentional control. In our study, the effect of rTPJ was marked especially when the type of previous trial was a distractor-present one. Thus, after encountering a salient distractor, stimulation of right TPJ appears to have boosted a mechanism for the rapid updating of an internal model, ultimately promoting top-down mechanisms for distractor filtering, in turn significantly reducing the distractor cost in the subsequent trial. Vice versa, albeit with substantially lesser impact (see Results), after an easy distractor-absent condition, TMS on right TPJ tends to relax the same filtering mechanisms, in turn tending to increase the distractor cost in the subsequent trial. This interpretation is supported by neuroimaging studies and dynamic causal modeling, demonstrating excitatory pathways from TPJ to FEF, and suggesting this pathway as the candidate neurofunctional substrate for how the contextual updating is translated into an attentional control signal that promotes distractor filtering to the benefit of behavior (Chambon et al., 2017; DiQuattro et al., 2014; DiQuattro & Geng, 2011; Geng & Vossel, 2013; Vossel et al., 2015).

Indeed, right FEF is known to be a key node of the dorsal attention network involved in exerting top-down control of attention and the filtering of task-irrelevant information, as demonstrated by functional neuroimaging studies (de Fockert et al., 2004; de Fockert & Theeuwes, 2012; Geng, 2014; Kane & Engle, 2002; Marini et al., 2016; Shimamura, 2000), neurophysiological (the frontal bias signal; Liesefeld, Liesefeld, & Zimmer, 2014; Vissers, van Driel, & Slagter, 2016; Vogel, McCollough, & Machizawa, 2005) and neuromodulatory (Cosman, Atreya, & Woodman, 2015; Lega et al., 2019) studies. Given the pivotal role of (r)FEF in top-down controlled allocation of attentional resources and the efficient filtering of irrelevant information, the input from right TPJ to FEF could mediate the delivery of predictive information to the frontal region, based on the acquisition of new contextual information (Vossel et al., 2015). In line with this view, Vossel et al. (2015) demonstrated that the trial-by-trial variability in connection strength from TPJ to FEF is context-sensitive, depending on the level of predictability when no a priori probability information is available and therefore must be inferred from accruing observations. Crucially, depending on the confirmation or violation of those predictions, TPJ suppressed or boosted activity in the FEF. We can here speculate that results observed in the present study (enhancing vs. decreasing the distractor cost as a function of the type of previous trial), may be the reflection of those different functional connectivity patterns between TPJ and FEF, which has been demonstrated to be highly sensitive to the probabilistic context.

Importantly, our previous TMS study demonstrated that stimulation of right FEF significantly interacts with the contingent trial history (Lega et al., 2019). Notably, in that case, TMS over rFEF eliminated the relative disadvantage of having experienced a distractor-absent condition in the previous trial, perhaps mimicking the actual encounter of a distractor on the previous trial. Here, instead, TMS of rTPJ seems to increase the impact of recent trial history in both directions: in particular, by significantly decreasing the cost of distractor when the previous trial was a distractor-present condition and relatively increasing the cost of distractor when the preceding trial was a distractor-absent condition. Together these results suggest the radically different nature of the mechanisms being affected by stimulation of the two different brain sites. Whereas, as we found in our prior study, rFEF stimulation may have enacted the sustained activation and maintenance of distraction-filtering mechanisms through the subsequent trial, hence resulting in a reduction of the distractor cost after a distractor-absent condition, in the present work rTPJ stimulation appears to have augmented the rapid updating of an internal model based on evidence gathered through

recent events, therefore rendering the system especially sensitive to the most recent episode. In the context of distractor filtering mechanisms, future investigations are needed to better clarify the role of TPJ in updating the model based on accumulated evidence. Importantly, in the present experiment, the distractor was present in 50% of the trials, rendering this context not ideal for building a predictive model with respect to the presence (or absence) of a distractor in a given trial and, notably, for using that model to maximize performance at the task. In this specific context, our results indicated that after rTPJ stimulation, more importance is given to each individual trial for the immediately subsequent adjustment of attentional processing, which is compatible with the hypothesis that rTPJ is responsible for a contextual updating mechanism that is based exclusively on the last event. Interestingly, here the modulation mainly occurs following a distractor-present trial, a condition wherein the potential behavioral advantage of dynamically boosting the proactive engagement of distractor suppression mechanisms outstands any putative detrimental effect even in the fully non-predictable context of the present experiment. However, to substantiate this tentative interpretation, it would be important to extend this investigation, for instance by manipulating the overall distractor probability, namely in a context where it is extremely useful to build a predictive model in order to optimize behavior. Testing whether phasic trial-by-trial adjustment or tonic contextual updating based on the overall accumulated evidence are supported by the same neural machinery (with a focus on right TPJ) represents an important challenge for future studies.

We did not find any significant effect of rTPJ on on-line attentional capture and distractor filtering mechanisms. This is not surprising, as traditionally right TPJ activation has been related to attentional mechanisms that reorient attention toward the appearance of unexpected but task-relevant stimuli (Corbetta et al., 2008; Corbetta & Shulman, 2002; Shomstein, 2012). Accordingly, neuroimaging studies have demonstrated that task-relevance is a crucial factor to evoke the activation of the right-lateralized ventral attention network (Indovina & Macaluso, 2007; Serences et al., 2005; Shulman et al., 2009). Therefore, TPJ activation is not due to saliency computation per se, as task-irrelevant salient stimuli do not activate TPJ but rather the dorsal attention network, FEF and IPS in particular (Geng & Mangun, 2011; Indovina & Macaluso, 2007; Kincade, 2005). In line with the current findings, previous TMS studies consistently demonstrated that rTPJ stimulation selectively affects contingent capture in the target-colored distractor condition (i.e., task relevant), but not in the nontarget-colored distractor condition (i.e., task irrelevant), as it was in our paradigm (Chang et al., 2013; Painter, Dux, & Mattingley, 2015).

Contrary to our expectations, stimulation of right MFG did not produce measurable effects either in the overall ability to filter-out salient distractors, or in the inter-trial context-dependent modulation of distractor suppression. Previous studies (see Marini et al., 2016) demonstrated that rMFG is particularly sensitive to the overall context of distraction, with different levels of activation depending on the overall frequency of potential distractors within the experimental session (e.g. 20% vs. 60%). When the likelihood of encountering a distractor is high, sustained activation of rMFG occurs, likely reflecting a tonic proactive mechanism for distractor filtering within a context of high potential conflict. In this view, it would be interesting to manipulate the overall frequency of distractor at the block/session level, thus invoking even stronger tonic proactive attentional control mechanisms. This type of manipulation may be better suited for inducing clear-cut behavioral changes following MFG stimulation. We can also speculate that time-locked 10 Hz TMS was highly effective in revealing the impact of stimulation on rapid trial-by-trial adjustments of distractor filtering mechanisms (as it was the case for TPJ). However, a more prolonged (off-line) stimulation affecting sustained attentional control mechanisms may be more suited to investigate the involvement of MFG in the current behavioral context. This may constitute the object of future studies.

Finally, as a cautionary note, in the present experiment the TMS targeting accuracy was ensured thanks to the use of the neuronavigation system, which allows to generate an individualized template-head model. Nonetheless, this may represent a limitation of the current study, since the use of the individual MRI together with the neuronavigation system might have been a more suitable choice. This aspect should be

borne in mind in the interpretation of the current results, especially considering the role of right parietal regions (both dorsal and ventral) in different attentional mechanisms. It would be interesting for future studies to further clarify the present results by adopting a different TMS localization approach.

In conclusion, our results show that stimulation of right TPJ exacerbates the effect of recent trial history. This likely reflects the enhanced updating of the predictive model that dynamically regulates proactive distractor-filtering mechanisms at the trial-by-trial level. These results align well with the role of TPJ in contextual updating of an internal model of the task context based on current stimuli (Chambon et al., 2017; DiQuattro & Geng, 2011; DiQuattro et al., 2014; Han & Marois, 2014; Mengotti et al., 2017; Vossel et al., 2015; for a review, see; Geng & Vossel, 2013), and in the detection of mismatches between expected and actual stimuli, by comparing external events with internal models and predictions (DiQuattro et al., 2014; Doricchi et al., 2010; Geng & Mangun, 2011; Summerfield & Egnér, 2009). Future research could fruitfully explore this issue further by testing the role of left TPJ as well. Indeed, in addition to the well-documented role of the right TPJ in stimulus-driven attentional control (Arrington, Carr, Mayer, & Rao, 2000; Corbetta et al., 2008; Corbetta & Shulman, 2002; Fox et al., 2006; Indovina & Macaluso, 2007; Kincade, 2005), mounting evidence shows that the left TPJ plays an important role in attentional control mechanisms (DiQuattro & Geng, 2011; Doricchi et al., 2010; Dugué et al., 2018; Geng & Vossel, 2013; Weidner, Krummenacher, Reimann, Müller, & Fink, 2009). Finally, previous TMS studies indicated right TPJ as a plausible candidate for the neural implementation of the inhibition of return (IOR) mechanisms (Bourgeois et al., 2013). In particular, right TPJ stimulation decreased IOR for manual (but not saccadic) responses selectively for ipsilateral targets (Bourgeois et al., 2013). In principle, in the present context, the significant reduction of the cost of distraction following a distractor-present condition, as shown in the current experiment, may be interpreted in terms of an effect of TMS on inhibition of return (IOR)-like mechanisms rather than in terms of contextual updating. Nonetheless, the temporal interval between the visual stimuli is known to be a critical factor for eliciting IOR (Lupiáñez, 2012). Notably, in the present study, the time interval between consecutive trials was more than 5 s, rendering this interpretation extremely unlikely. Still, we set out to test this possibility directly with ad-hoc analyses (not reported in the present paper for the sake of brevity) showing that no IOR-like phenomena were elicited when distractors appeared in the same (vs. different) hemifield or spatial location in two consecutive trials (nor were modulations emerging following TMS delivery at either site). That said, it would be interesting for future investigations to adopt the same paradigm as the one used here, while manipulating the time interval between the presentation of two consecutive distractor trials, in order to test for the potential contribution of IOR-like mechanisms in a context where distractor suppression mechanisms are strongly engaged. These observations, together with the present findings, will help clarify the brain network responsible for detecting and flexibly responding to distracting stimuli, providing further evidence of the neural underpinning of distraction-filtering mechanisms.

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