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## Probing the neural mechanisms for distractor filtering and their history-contingent modulation by means of TMS

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# 1                    **Probing the neural mechanisms for distractor filtering and their history-** 2                    **contingent modulation by means of TMS**

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29                    wrote the paper; all authors provided feedback on early versions of the manuscript.

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37 **ABSTRACT**

38 In visual search, the presence of a salient, yet task-irrelevant, distractor in the stimulus array  
39 interferes with target selection and slows-down performance. Neuroimaging data point to a key  
40 role of the fronto-parietal dorsal attention network in dealing with visual distractors; however, the  
41 respective roles of different nodes within the network and their hemispheric specialization are still  
42 unresolved. Here, we used transcranial magnetic stimulation (TMS) to evaluate the causal role of  
43 two key regions of the dorsal attention network in resisting attentional capture by a salient  
44 singleton distractor: the frontal eye field (FEF) and the cortex within the intraparietal sulcus (IPS).  
45 The task of the participants (male/female human volunteers) was to discriminate the pointing  
46 direction of a target arrow while ignoring a task-irrelevant salient distractor. Immediately after  
47 stimulus onset, triple-pulse 10Hz TMS was delivered either to IPS or FEF on either side of the  
48 brain. Results indicated that TMS over the right FEF significantly reduced the behavioral cost  
49 engendered by the salient distractor relative to left FEF stimulation. No such effect was obtained  
50 with stimulation of IPS on either side of brain. Interestingly, this FEF-dependent reduction in  
51 distractor interference interacted with the contingent trial history, being maximal when no  
52 distractor was present on the previous trial relative to when there was one. Our results provide  
53 direct causal evidence that the right FEF houses key mechanisms for distractor filtering, pointing  
54 to a pivotal role of the frontal cortex of the right hemisphere in limiting interference from an  
55 irrelevant but attention-grabbing stimulus.

56

57 *Key words:* distractor filtering, dorsal attentional network, transcranial magnetic stimulation,  
58 frontal eye field (FEF), intraparietal sulcus (IPS)

59

60 **SIGNIFICANT STATEMENT**

61 Visually conspicuous stimuli attract our attention automatically and interfere with performance by  
62 diverting resources away from the main task. Here, we applied TMS over four fronto-parietal  
63 cortex locations (FEF and IPS in each hemisphere) to identify regions of the dorsal attention  
64 network that help limit interference from task-irrelevant, salient distractors. Results indicate that  
65 the right FEF participates in distractor-filtering mechanisms that are recruited when a distracting  
66 stimulus is encountered. Moreover, right FEF implements adjustments in distraction-filtering  
67 mechanisms following recent encounters with distractors. Altogether, these findings indicate a  
68 different hemispheric contribution of the left vs. right dorsal frontal cortex to distraction filtering.  
69 This study expands our understanding of how our brains select relevant targets in the face of task-  
70 irrelevant, salient distractors.

71

72

73 **INTRODUCTION**

74 Visual selective attention supports an individual's ability to select relevant information while  
 75 disregarding irrelevant but attention-grabbing stimuli (Forster & Lavie, 2008; Jonides & Yantis,  
 76 1988; Marini et al., 2013; Yantis & Jonides, 1990). Evidence that attention is involuntarily captured  
 77 by salient stimuli comes, among others, from studies using visual search arrays with salient  
 78 *singleton* distractors, such as a uniquely colored stimulus in an array of differently colored items  
 79 (Theeuwes, 1992; Theeuwes & Burger, 1998; Theeuwes & Godijn, 2002). The presence of a  
 80 singleton distractor in a search array results in an unwanted shift of attention to the salient  
 81 stimulus (attentional capture effect), as indexed by a measurable performance cost relative to  
 82 trials without the singleton distractor. Stimulus-driven mechanisms responsible for the attentional  
 83 capture effects are antagonized by goal-driven mechanisms that guide attention towards the  
 84 relevant target stimulus and suppress distractors (Chelazzi et al., 2010; Marini et al., 2016; Müller  
 85 & Ebeling, 2008; Reynolds & Chelazzi, 2004), although the cognitive and neural mechanisms that  
 86 support distractor filtering are still under debate.

87 Distractor filtering, which consists in the elimination, or at least the attenuation, of the  
 88 behavioral costs engendered by irrelevant yet salient stimuli, has received mounting interest in  
 89 the recent years (Chelazzi et al., 2019). Different putative mechanisms for distractor filtering have  
 90 been proposed depending on the adopted experimental paradigm and behavioral context  
 91 (Chelazzi et al., 2019). These mechanisms include proactive control (Cosman et al., 2018; Geng,  
 92 2014; Marini et al., 2013, 2016), habituation of capture (Neo & Chua, 2006; Pascucci & Turatto,  
 93 2015; Turatto et al., 2017, 2018), inter-trial priming (Geyer et al., 2008; Müller et al., 2010), and  
 94 implicit distractor probability learning (Di Caro et al., 2019; Ferrante et al., 2018; Goschy et al.,  
 95 2014; Sauter et al., 2019, 2018; B. Wang & Theeuwes, 2018b, 2018a). Despite the abundance of  
 96 behavioral evidence about specific task conditions and behavioral contexts wherein distractor

97 suppression occurs, much less is known about the underlying neural mechanisms (Donohue et al.,  
 98 2018; Egeth et al., 2010; Folk & Remington, 2010; Gaspar & McDonald, 2014; Geng, 2014; A. M.  
 99 Liesefeld et al., 2014; H. R. Liesefeld et al., 2017; Marini et al., 2016; Seidl et al., 2012). Therefore,  
 100 the present study sought to characterize the neural machinery for distractor filtering by  
 101 investigating the causal role of different sub-regions within the dorsal attention network.

102 Numerous functional imaging studies demonstrated that attentional control in the  
 103 presence of potential distraction is supported by the dorsal (mostly bilateral) fronto-parietal  
 104 attention network, whose core regions include the frontal eye field (FEF) and the posterior parietal  
 105 cortex, notably tissue within the intraparietal sulcus (IPS) (Corbetta & Shulman, 2002; de Fockert  
 106 et al., 2004; de Fockert & Theeuwes, 2012; DiQuattro et al., 2014; Leber, 2010; Lee & Geng, 2017;  
 107 Marini et al., 2016; Serences et al., 2005, 2004; Talsma et al., 2009). These anatomical locations  
 108 align well with electrophysiological evidence in non-human primates showing that both target  
 109 selection and distractor suppression mechanisms involve parietal (Ipata et al., 2006) and  
 110 prefrontal cortex (for a specific contribution of FEF in distractor suppression, see Cosman et al.  
 111 2018), although neural responses to salient distractors are more greatly suppressed and more  
 112 closely correlated with performance in prefrontal, rather than parietal cortex (Suzuki & Gottlieb,  
 113 2013).

114 Brain imaging studies in humans also reported a correlation between frontal (but not  
 115 parietal) neural activity and the magnitude of distractor interference, strongly supporting a role  
 116 for the frontal cortex in actively preventing the interference from irrelevant distractors (de Fockert  
 117 et al., 2004; de Fockert & Theeuwes, 2012; Marini et al., 2016). Consistently, ERP studies also  
 118 converge in indicating a prominent role of frontal areas in attentional control (Brignani et al.,  
 119 2009; Grent-'t-Jong & Woldorff, 2007; Leblanc et al., 2008; A. M. Liesefeld et al., 2014; Ptak et al.,  
 120 2011; Shomstein et al., 2012). These findings also revealed an orderly temporal structure of neural

121 signatures during the control of spatial attentional allocation, with attentional control signals first  
 122 elicited at the level of the frontal lobe, followed by activity in the parietal lobe. This temporal  
 123 advantage for the frontal over the parietal signals likely reflects processes involved in attentional  
 124 deployment, but also in target selection and conflict control. Taken together, these results seem  
 125 to indicate a leading contribution of the frontal areas in monitoring (potential) conflict and  
 126 proactively preventing or reactively abating distraction. However, an inherent limitation of these  
 127 studies is the inability to reveal any causal organization in the described relationship between  
 128 brain activity and behavioral performance. In order to probe causal relationships between brain  
 129 and behavior, non-invasive brain stimulation techniques are the most suitable choice (Pascual-  
 130 Leone et al., 2000). Cosman and colleagues (2015) demonstrated that anodal transcranial direct-  
 131 current stimulation (tDCS) over pre-frontal cortex enhanced the ability of participants to overcome  
 132 distraction by decreasing the RT-cost associated with a salient but task-irrelevant item. Along the  
 133 same lines, by using repetitive TMS over posterior parietal cortex (PPC), Hodsoll and colleagues  
 134 found that TMS over the right PPC, but not the left PPC, significantly reduced the RT-cost of  
 135 distraction. Moreover, the fronto-parietal network is causally involved in filtering-out not only  
 136 perceptually salient, but also conflicting distractors, as demonstrated by modulations in the  
 137 interference elicited by task-irrelevant flanker stimuli after tDCS of either pre-frontal (Zmigrod et  
 138 al., 2016) or parietal cortex (Kajimura & Nomura, 2015; Weiss & Lavidor, 2012).

139 Brain stimulation studies have revealed that the parietal and pre-frontal cortices are  
 140 involved in distractor filtering. However, due to the poor spatial resolution of tDCS and the lack of  
 141 TMS or tDCS studies that directly compared the two crucial nodes of the dorsal fronto-parietal  
 142 network, namely the FEF and IPS, it remains to be established whether distractor filtering is more  
 143 distinctively supported by one or the other node of this network, or equally by both. Likewise, the  
 144 available evidence is highly inconclusive as to whether the right and left dorsal attention networks

are equally involved in distractor filtering. In the present study, we used TMS to comparatively investigate the causal role in distraction filtering of FEF and IPS on either side of the brain. Our general hypothesis was that the dorsal fronto-parietal network is causally involved in distraction filtering, consistent with evidence in the literature (Chelazzi et al., 2019), but that this function might be more strongly supported by either node in the network. In particular, in light of previous neuroimaging observations (de Fockert et al., 2004; de Fockert & Theeuwes, 2012; Marini et al., 2016; Melloni et al., 2012) and the established temporal dynamics within the fronto-parietal network, demonstrated by ERPs studies (Brignani et al., 2009; Grent-'t-Jong & Woldorff, 2007; Leblanc et al., 2008; A. M. Liesefeld et al., 2014; Ptak et al., 2011; Shomstein et al., 2012), we might expect a more distinctive involvement of frontal regions in distractor suppression mechanisms, as indexed by a stronger modulation in the cost of distraction following FEF stimulation.

Cross-trial contingencies – such as the presence or absence of distractors in consecutive trials – are well-known to modulate distraction filtering: for example, the reaction-time (RT) cost engendered by a salient distractor is larger when a distractor was absent (vs. present) in the immediately preceding trial (Geyer et al., 2008; Marini et al., 2013). A neuro-functional architecture for this effect may consist of an increase in top-down control following distractor encounters (Botvinick et al., 2001; Kerns, 2004), mediated by increased activity in the fronto-parietal circuit (FEF and IPS, see Walsh et al., 2011). This view finds support in neuro-stimulation studies (Hodsoll et al., 2009; Soutschek et al., 2013) showing that the modulation of activity in the right posterior parietal cortex by means of TMS affected performance during conflict tasks, with the effect being strongly modulated as a function of what happened in the previous trial. Hodsoll and colleagues (2009) used an additional singleton paradigm to demonstrate that inhibitory 1-Hz TMS over the right PPC, but not left PPC, reduced the behavioral cost of a color-singleton



distractor. Crucially, this lessening of distractor interference was mostly due to the elimination of priming effects between target and distractor singletons on consecutive trials. In this context, we therefore hypothesized an effect of TMS that varies depending on recent trial history, namely depending on the state of the brain in the instant when it encounters a distractor. This idea also fits well with the notion of state dependency, whereby the effects of TMS on behavioral performance depend not only on the stimulation parameters themselves, but also on the brain's 'state' when stimulation is applied (Silvanto & Cattaneo, 2017; Silvanto & Pascual-Leone, 2008). Based on this evidence, here we formulated the additional hypothesis that modulations of distraction filtering by cross-trial contingencies may likewise be mediated by the dorsal fronto-parietal network, and therefore that FEF and/or IPS stimulation might alter such history-dependent modulations of distractor filtering. Therefore, if FEF and/or IPS are involved also in the regulation of cross-trial dynamics of distractor-filtering, we expected to identify an interaction between TMS stimulation on a given trial and the presence vs. absence of a distractor in the preceding trial, a possibility that we addressed with the present work.

183

## 184 **METHODS**

### 185 **Participants**

186 Thirty-two participants took part in the experiment (22 F; mean age = 23.56, SD = 3.44). Two of  
 187 them had to be excluded: One participant did not complete the task because FEF stimulation  
 188 induced slight movements of the contralateral hand, which interfered with the task; another  
 189 participant was excluded because of near-chance responses (mean accuracy: 58%). Therefore,  
 190 data from 30 participants (20 females, mean age = 23.4, SD = 3.24) were used for the analyses  
 191 reported below. We would like to state candidly that, following the initial reviewing of our study,

192 in compliance with the reviewers' recommendation, we increased the original sample size, from N  
 193 = 20 to the final N = 30 subjects. To the benefit of complete transparency, the key statistical  
 194 results on the original sample are available online at <https://osf.io/4ke56/>, stored on the Open  
 195 Science Framework data sharing platform. All participants were right-handed and with normal or  
 196 corrected-to-normal visual acuity and normal color vision. Prior to the TMS experiment, each  
 197 subject filled-in a questionnaire to evaluate eligibility for TMS. None of the participants reported  
 198 any contraindications for TMS use (Rossi et al., 2009). Written informed consent was obtained  
 199 from all participants prior to the beginning of the experiment. The study protocol was approved by  
 200 the local ethical committee and the experiment was conducted in accordance with the Declaration  
 201 of Helsinki.

## 202 **Materials and stimuli**

203 The protocol was adapted from the additional singleton paradigm (Theeuwes, 1992). A version of  
 204 the paradigm similar to the one used in the current experiment has been used before in our lab  
 205 (Ferrante et al., 2018). The visual search display consisted of four stimuli (one per visual quadrant)  
 206 presented equidistantly from one another and centered on a central fixation point (eccentricity: 4  
 207 degrees). All stimuli were composed of two green or red triangles ( $1^\circ \times 1^\circ$  each) presented on a  
 208 light grey background. In 50% of trials all display items were of the same color (e.g., red;  
 209 distractor-absent condition), whereas in the remaining 50% of trials three items were of the same  
 210 color (e.g., red) and the remaining item (additional singleton) was of the alternative color (e.g.,  
 211 green; distractor-present condition). The target was defined as the only item in the display with  
 212 both triangles pointing in the same direction (both up or both down, i.e. a double arrow-head),  
 213 whereas the singleton distractor, when present, was a color-singleton stimulus with both triangles  
 214 pointing outwardly. The remaining stimuli (non-targets or fillers) were always of the same color as  
 215 the target and with both triangles pointing inwardly (see Fig. 1A).

## 216 Procedure

217 Participants were seated in front of a 17" CRT monitor (spatial resolution of 1280 x 1024-pixel and  
 218 a refresh rate of 75 Hz) at a distance of 57 cm, in a dimly illuminated, silent room. A chin rest was  
 219 used to keep the viewing distance constant during the whole session. Each trial began with a  
 220 fixation point displayed in isolation for 1000 ms, and this was then accompanied for 700 ms by an  
 221 array of four placeholders, which were identical to non-targets. At the end of the 700-ms period,  
 222 one of the placeholders was replaced by the target and, on 50% of the trials, a different  
 223 placeholder was replaced by the singleton distractor (Ferrante et al., 2018; Tommasi et al., 2015).  
 224 This array remained visible for 50 ms and was followed by a blank screen until the participant  
 225 responded or 2000 ms had elapsed, whichever came first. The subsequent trial started after a  
 226 4000-ms inter-trial interval (Fig. 1B). The participants' task was to indicate as quickly and as  
 227 accurately as possible whether the target element was pointing up or down by pressing '1' for 'up'  
 228 or '2' for 'down' on a numeric keypad (or vice-versa; counterbalanced across participants). The  
 229 experiment included two sessions conducted on two different days. In each session, participants  
 230 completed a practice block of 24 trials to familiarize with the task, followed by 6 experimental  
 231 blocks (one per TMS condition).

232 Each block consisted of 72 trials, 36 of which were distractor-present and 36 distractor-  
 233 absent. Within each block, the target and the singleton distractor were presented equally often at  
 234 any given spatial location. The order of blocks was pseudo-randomized in such a way that in the  
 235 first session the six different TMS conditions were equally distributed across participants (in order  
 236 to spread out any potential learning effect equally across TMS conditions). The second session was  
 237 identical to the first one, except that the order of blocks was reversed relative to the first session  
 238 (in order to minimize any carry over effects related to stimulation site). Each experimental session  
 239 lasted approximately 2 hours.

## 240 Transcranial magnetic stimulation

241 Online neuronavigated TMS was delivered using a Magstim Rapid2 stimulator (Magstim Co Ltd,  
 242 Whitland, UK) connected to a 70-mm butterfly coil. Targeted sites in different blocks were over  
 243 the left and right IPS and over the left and right FEF. In order to control for any possible non-  
 244 specific effects due to lateralized TMS, we identified two suitable sham conditions in a region on  
 245 the scalp located between IPS and FEF of the left and right hemisphere, respectively. This yielded  
 246 six different TMS conditions corresponding to the six scalp sites of stimulation (four with active  
 247 stimulation and two with sham stimulation). The four active TMS sites were localized by means of  
 248 stereotaxic navigation on individual estimated magnetic resonance images (MRI) obtained through  
 249 a 3D warping procedure fitting a high-resolution MRI template with the participant's scalp model  
 250 and craniometric points (Softaxic, EMS, Bologna, Italy). Neuronavigation used anatomical Talairach  
 251 coordinates (Talairach & Tournoux, 1988) obtained by converting the MNI coordinates of the sites  
 252 of interest from a recent meta-analysis of functional MRI studies of eye movements (Zhou & Shu,  
 253 2017). Coordinates were  $x=-36$ ,  $y=-1$ ,  $z=48$  and  $x=36$ ,  $y=-1$ ,  $z=48$  for left and right FEF, respectively,  
 254 and  $x=-30$ ,  $y=-53$ ,  $z=49$  and  $x=30$ ,  $y=-53$ ,  $z=49$  for left and right IPS, respectively (Fig. 1C).

255 Since the existing literature shows that FEF can be localized based on distance from  
 256 primary motor cortex (M1) (Ro et al., 1999), as an additional step we measured the anatomical  
 257 distance on the scalp between the targeted, putative FEF site and the corresponding M1 within  
 258 each hemisphere. After localizing the area of primary motor cortex that produced the most robust  
 259 contraction of the contralateral hand, a scalp marking was made on each subject over this location  
 260 (both over the right and left M1). Then, after localizing the putative FEF hotspots by means of the  
 261 neuro-navigation approach, as previously described, we calculated the distance between putative  
 262 FEF and M1 in each hemisphere, separately for each participant. Across subjects, the mean  
 263 distances between FEF and M1 were 2.76 cm (right) and 2.78 cm (left). More importantly, once we

264 obtained our behavioral indexes of TMS-induced modulation of performance (see below), we  
 265 asked whether such modulation was affected by the distance across individual participants  
 266 between the two critical sites (M1 and putative FEF). To anticipate, by applying this method and a  
 267 correlational approach, we obtained evidence to indicate that the effects of TMS across  
 268 participants tended to be greatest when applied at a certain distance anteriorly from the  
 269 functionally identified M1 site (see below).

270 The resting motor threshold (rMT) was determined using a software-based “adaptive  
 271 method” developed by Awiszus (2003) (Motor Threshold Assessment Tool, MTAT, version  
 272 2.0: <http://www.clinicalresearcher.org/software.htm>). Any visible muscle twitch was entered in  
 273 the software as a “valid response”. During the experiment, TMS was delivered at 100% of the  
 274 individual rMT (mean intensity = 51% of the maximum stimulator output). For the left FEF/IPS and  
 275 right FEF/IPS, the coil was initially oriented with an angle of approximately 45° from the nasion-  
 276 inion line and the handle pointing outwards, and hence adjusted for each participant in order to  
 277 minimize discomfort. For the two sham conditions the coil was held perpendicular to the scalp in  
 278 order to ensure that the magnetic field did not stimulate the underlying cortex. Three TMS pulses  
 279 were delivered at 10 Hz (pulse gap of 100 ms) starting 100 ms after search array onset (see Fig.  
 280 1B). We used triple-pulse 10 Hz TMS following previous studies showing that these stimulation  
 281 parameters were effective in modulating the underlying cortical activity (Kadosh et al., 2010; Saad  
 282 & Silvanto, 2013). Triple-pulse 10 Hz TMS starting at 100 ms covered a time-window (100-300 ms)  
 283 that is crucial for attentional capture effects and distractor suppression mechanisms, as shown by  
 284 human scalp electrophysiology (Jannati et al., 2013; H. R. Liesefeld et al., 2017; McDonald et al.,  
 285 2013). The software Open-Sesame (Mathôt et al., 2012) was used for stimulus presentation, data  
 286 collection and TMS triggering.

287 [Insert Fig. 1 about here]

## 288 Statistical analysis

289 Reaction times (RTs) were log-transformed prior to the analysis in order to assuage deviations  
 290 from normality (before transformation: skewness = 2.23, kurtosis = 5.52; after transformation:  
 291 skewness = -0.05, kurtosis = 0.44). Only correct-response trials were included in the RT analysis (a  
 292 total of 5.8 % of trials were excluded). Linear mixed-effect models were used as the main  
 293 statistical procedure (Baayen et al., 2008). We set up each model following Barr, Levy, Scheepers,  
 294 and Tily's (2013) recommendation to model the maximal random-effects structure justified by the  
 295 experimental design. Statistical significance was tested with the F-test with Satterthwaite  
 296 approximation of degrees of freedom. All the models were estimated using R (R Development  
 297 Core Team, 2016) and the *lme4* package (version 1.1-12) (Bates et al., 2014). When appropriate,  
 298 post-hoc tests were conducted using the R-package *phia* (version 0.2-0, De Rosario-Martinez,  
 299 2015) and applying the Bonferroni-Holm correction for multiple comparisons.

300 TMS effects are best understood when comparing each active TMS condition with the  
 301 corresponding (right or left) sham stimulation. An advantage of having two sham conditions, as  
 302 opposed to only one, is to subtract-out any potential non-specific TMS effect, such as the  
 303 lateralized click of the coil associated with the TMS stimulation. Indeed, previous studies  
 304 demonstrated that the clicking sound of the TMS pulse induces a shift of covert spatial attention  
 305 to the corresponding side of space, thus facilitating target detection ipsilateral to the stimulation  
 306 (Duecker & Sack, 2013). In addition to the RT analysis, we conducted an accuracy analysis on all  
 307 conditions (see Table 1). However, since no significant effect of TMS emerged from the accuracy  
 308 analysis, we will not report those results except for the sham conditions (see below). Finally, for  
 309 significant effects, effect size was computed as Cohen's  $f^2$  (Selya et al., 2012), which uses residual  
 310 variance from the model to estimate effect size. Since mixed-effect models have two different  
 311 types of  $R^2$  (variance explained), the marginal  $R^2$ , which represents the variance explained by the

fixed effects, and the conditional  $R^2$ , which represents the variance explained by the entire model, whenever both fixed and random effects were included in the model two different  $f^2$  were calculated for each effect, namely the  $f^2_m$  (marginal) and the  $f^2_c$  (conditional). Nonetheless, for multi-level models effect sizes calculated using residual variance and proportion of explained variance should be interpreted with caution because the addition of variables to the model may increase residual variance, resulting in negative estimates of explained variance and even of effect size (Snijders & Bosker, 1994).

Table 1. Mean accuracy in percentage (%) for each TMS condition as a function of Distractor presence (present vs. absent) and Brain hemisphere (left vs. right). The standard deviation for each condition is indicated in brackets.

	Left hemisphere		Right hemisphere	
	Distractor present	Distractor absent	Distractor present	Distractor absent
Sham	91.8 % (6.8)	96.4 % (3.8)	91.5 % (8.0)	96.1 % (5.1)
FEF	91.6 % (6.6)	96.6 % (4.3)	92.3 % (7.5)	97.5 % (2.8)
IPS	91.2 % (7.5)	96.8 % (4.3)	92.4 % (6.4)	97.2 % (2.9)

## RESULTS

**Behavioral effects.** To ensure that the adopted paradigm was suitable for the given purposes, we first tested the interfering effect of distracting visual stimuli on task performance in the absence of active TMS stimulation (i.e., restricting the analysis to the sham condition). The Brain hemisphere (left vs. right), Distractor presence (present vs. absent) and their interaction were entered as fixed-effect factors in a linear mixed model that predicted log-transformed RTs on correct-response trials. Intercepts and slope for the interaction between Brain hemisphere and Distractor presence were also included in the model as random-effect factors across participants. This analysis revealed a significant main effect of Distractor presence,  $F(1,28.85) = 161.32$ ,  $p < .001$  ( $f^2_m = .071$ ,  $f^2_c = .14$ ), reflecting faster responses in the distractor-absent condition ( $M = 361$  ms) compared to the distractor-present condition ( $M = 456$  ms). The main effect of Brain hemisphere was not

334 significant,  $F(1,28.51) < 1$ ,  $p = .88$ . Importantly, the interaction between Distractor presence and  
 335 Brain hemisphere was also non-significant,  $F(1, 85.98) < 1$ ,  $p = .40$ , indicating that the effect of  
 336 distractor did not differ significantly between the two control sham conditions (see Fig. 2A).  
 337 Similarly, a mixed logistic model was estimated using accuracy as the dependent variable. This  
 338 analysis (see Fig. 2B) revealed a significant main effect of Distractor presence,  $\chi^2(1) = 34.37$ ,  $p <$   
 339  $.001$ , and no other significant effects (main effect of Brain hemisphere:  $\chi^2(1) < 1$ ,  $p = .54$ ;  
 340 interaction Distractor presence by Brain hemisphere:  $\chi^2(1) < 1$ ,  $p = .94$ ). Contrast analysis showed  
 341 that when a distractor was present the participants' accuracy rates were lower (94%) compared to  
 342 the no-distractor condition (98%),  $z = -4.75$ ,  $p < .001$  (see Fig. 2B).

343       As a second step, we evaluated whether, and to what degree, experiencing a distractor in  
 344 the previous trial modulated distractor interference on the current trial. Indeed, behavioral  
 345 research has demonstrated larger distractor costs on a given trial  $N$  when no distractor was  
 346 presented (vs. when it was presented) on the previous trial  $N-1$  (Geyer et al., 2008; Müller et al.,  
 347 2010). Note that for this analysis trials following incorrect-response trials were omitted, as well as  
 348 incorrect-response trials (8.15% of total trials). Log-transformed RTs were analyzed with a linear  
 349 mixed model that included Brain hemisphere (left vs. right), Distractor presence (present vs.  
 350 absent) and Type of previous trial (distractor-present vs. distractor-absent) as fixed-effect factors,  
 351 and random intercepts and slope for factors Brain hemisphere, Distractor presence and Type of  
 352 previous trial within participants. The analysis revealed a significant main effect of Distractor  
 353 presence,  $F(1,28.7) = 152.07$ ,  $p < .001$ , ( $f^2_m = .073$ ,  $f^2_c = .14$ ) and a quasi-significant effect of Type of  
 354 previous trial,  $F(1,73.8) = 3.81$ ,  $p = .055$ . Importantly, and as predicted, the analysis also showed a  
 355 significant interaction between Distractor presence and Type of previous trial,  $F(1,7390.2) = 9.37$ ,  
 356  $p = .002$ , ( $f^2_m = .0005$ ,  $f^2_c = .001$ ). This interaction emerged because the distractor cost was larger  
 357 when a distractor was absent in the previous trial ( $M = 103$  ms) compared to when it was present



(M = 87 ms) (Fig. 2C). Importantly, this effect was not significantly modulated by Brain hemisphere, as indicated by a non-significant three-way interaction between Distractor presence, Type of previous trial and Brain hemisphere,  $F(1,7384.9) < 1$ ,  $p = .50$ . All of the other effects or interactions were not significant: the main effect of Brain hemisphere,  $F(1,28) < 1$ ,  $p = .82$ ; the interaction Brain hemisphere by Distractor presence,  $F(1,7377.3) < 1$ ,  $p = .66$ , and the interaction Brain hemisphere by Type of previous trial,  $F(1,7383.4) < 1$ ,  $p = .69$ . Finally, a mixed-effect logistic model was estimated using accuracy as the dependent variable. This analysis revealed a significant main effect of Distractor,  $\chi^2(1) = 35.29$ ,  $p < .001$ , as before. The interaction between Distractor presence and Type of previous trial was non-significant,  $\chi^2(1) = 1.52$ ,  $p = .21$ . Contrast analysis showed that the cost of distractor did not differ reliably depending on the absence vs. presence of a distractor in the previous trial (cost of distraction = 4.9 % and 2.8%, respectively),  $z = 1.62$ ,  $p = .10$  (see Fig. 2D). No other main effects or interactions were significant: the main effect of Brain hemisphere,  $\chi^2(1) < 1$ ,  $p = .70$ ; the interaction Distractor presence by Brain hemisphere,  $\chi^2(1) < 1$ ,  $p = .78$ ; the interaction Brain hemisphere by Type of previous trial,  $\chi^2(1) < 1$ ,  $p = .64$ , and the three-way interaction Distractor presence by Type of previous trial by Brain hemisphere,  $\chi^2(1) = 1.12$ ,  $p = .29$ .

[Insert Fig. 2 about here]

**Effect of TMS on visual search.** We tested the effect of TMS on distractor filtering mechanisms using a linear mixed model that predicted log-transformed RTs on correct-response trials. The experimental factors TMS (sham vs. FEF vs. IPS), Distractor presence (present vs. absent), Brain hemisphere (left vs. right), and all their interactions were included as fixed effects. Random coefficients across participants were estimated for intercept and for factors TMS, distractor

presence and brain hemisphere. The omnibus analysis revealed a significant main effect of Distractor presence,  $F(1,28.9) = 188.65$ ,  $p < .001$ , ( $f^2_m = .065$ ,  $f^2_c = .13$ ), indicating that participants were overall faster in the distractor-absent condition ( $M = 361$  ms) compared to the distractor-present condition ( $M = 451$  ms), with an average distractor cost of 90 ms. Crucially, the three-way interaction TMS by Brain hemisphere by Distractor presence was significant,  $F(2,24116.7) = 4.20$ ,  $p = .01$ , ( $f^2_m = .0002$ ,  $f^2_c = .0004$ ) (see Table 2). Contrast analysis showed that the effect of the right FEF stimulation (i.e., difference in distractor cost between right sham and right FEF TMS conditions) was significantly different from the effect of the left FEF stimulation (i.e., difference in distractor cost between left sham vs. left FEF TMS conditions),  $t = 2.883$ ,  $p = .003$ : This reflected reduced distractor cost following right, but not left, FEF stimulation. The distractor cost associated with IPS stimulation did not significantly differ between brain hemispheres,  $t = 1.168$ ,  $p = .24$ , as well as the difference between IPS and FEF TMS stimulation between the left and the right hemisphere,  $t = 1.718$ ,  $p = .09$  (see Fig. 3A).

Table 2. Summary of the linear mixed model predicting the effect of TMS on distractor filtering mechanisms as a function of stimulation site and brain hemisphere

	Num DF	Den DF	F	p
Distractor presence	1	28.9	188.651	<.001***
TMS	2	29.1	<1	.62
Brain hemisphere	1	28.9	1.5934	.22
Distractor presence x TMS	2	24122.5	2.8440	.06
Distractor presence x brain hemisphere	1	24123.0	2.8074	.09
TMS x brain hemisphere	2	24117.3	8.0674	<.001***
Distractor presence x TMS x brain hemisphere	2	24116.7	4.2069	.01*

\*\*\*  $p < .001$ , \*  $p < .05$

To further explore the significant three-way interaction, we performed follow-up analyses separately for each hemisphere. The left hemisphere analysis revealed a non-significant

400 interaction TMS by Distractor presence,  $F(2, 53.75) < 1, p = .85$ . On the contrary, the right  
 401 hemisphere analysis indicated that the interaction TMS by Distractor presence was significant,  $F(2,$   
 402  $34.89) = 4.58, p = .017, (f^2_m = .0005, f^2_c = .0009)$  (see Table 3). Contrast analysis confirmed that the  
 403 interaction effect reflected a significant decrease in the distractor cost with FEF vs. Sham  
 404 stimulation (the average distractor cost decreased by 23 ms;  $t = 3.023, p = .004$ ). The distractor  
 405 cost did not significantly differ either for the sham vs. IPS contrast,  $t = 1.369, p = .18$ , or for the IPS  
 406 vs. FEF contrast,  $t = 1.491, p = .14$  (see Fig. 3A).

407 To further investigate whether the reduction in the distractor cost following right FEF  
 408 stimulation was due to a relative RT-increase in the distractor-absent condition, to a relative RT-  
 409 decrease in the distractor-present condition, or to a combination of both, we conducted post-hoc  
 410 comparisons. These revealed that FEF stimulation reliably reduced RTs compared to sham  
 411 selectively in the distractor-present condition,  $\chi^2(1) = 8.01, p = .027$ . The contrast between FEF and  
 412 IPS stimulation in the distractor-present condition revealed a slight trend towards significance,  
 413  $\chi^2(1) = 5.79, p = .080$ . All other comparisons were far from significant, all  $ps > .56$  (see Fig. 3B and  
 414 3C).

416 Table 3. *Summary of the linear mixed model predicting the effect of TMS on distractor filtering*  
 417 *mechanisms, separately computed for left and right hemisphere*

		Num DF	Den DF	F	p
Right hemisphere	Distractor presence	1	28.803	218.019	<b>&lt;.001<sup>***</sup></b>
	TMS	2	28.901	2.4004	.10
	Distractor presence x TMS	2	34.893	4.5807	<b>.017<sup>*</sup></b>
Left hemisphere	Distractor presence	1	28.924	150.384	<b>&lt;.001<sup>***</sup></b>
	TMS	2	29.058	<1	.84
	Distractor presence x TMS	2	53.750	<1	.85

418 <sup>\*\*\*</sup>  $p < .001$ , <sup>\*</sup>  $p < .05$

419

420 An important question to ask is whether any effects of TMS on the distractor cost depend  
 421 critically on the spatial position of the distractor and/or of the target in the given search display.  
 422 Therefore, we analyzed RTs in the distractor-present condition as a function of whether the target  
 423 and distractor appeared in the right or left visual field, i.e., ipsilateral or contralateral to the  
 424 stimulation (only right TMS conditions were considered in this analysis). We implemented a linear  
 425 mixed model with the experimental factors TMS (sham vs. FEF vs. IPS), Target side (right vs. left)  
 426 and Distractor side (right vs. left) as fixed effects. The random effect structure included the  
 427 random intercept for subject, as well as the by-subject random slope for TMS, Target side and  
 428 Distractor side. The analysis indicated a significant interaction between Target side and Distractor  
 429 side,  $F(1,5821) = 32.39$ ,  $p < .001$ , reflecting longer RTs when target and distractor were on the  
 430 same side ( $M = 462$  ms) compared to opposite sides ( $M = 440$  ms), presumably due to greater  
 431 competition in the former condition relative to the latter. Crucially, TMS did not interact with  
 432 either Target side,  $F(2,5819.9) < 1$ ,  $p = .99$ , or Distractor side  $F(2,5823.1) < 1$ ,  $p = .48$ , or their  
 433 interaction  $F(2,5821.5) < 1$ ,  $p = .39$ , indicating that the reduction in the distractor cost associated  
 434 with right FEF stimulation occurred irrespective of the visual field wherein target and distractor  
 435 stimuli were respectively presented.

436 An additional analysis was performed to assess whether the chosen coordinates for the FEF  
 437 stimulation site were optimal with respect to the putative cortical location of FEF at the level of  
 438 individual participants. Here, coordinates for the FEF site were derived from the existing literature  
 439 (Zhou & Shu, 2017). However, it is also known that the distance between FEF and the primary  
 440 motor cortex (M1) is around 2 cm in humans (Müri et al., 1991; Ro et al., 1999). Because the  
 441 behavioral effects of TMS over right (and left) FEF varied considerably across participants, and so  
 442 did the scalp distance between M1 and the stimulated FEF site, we hypothesized that the

443 strongest behavioral effects of FEF stimulation might have occurred in those participants for  
 444 whom the M1-FEF distance was around the expected, anatomically-plausible value of 2 cm (due to  
 445 more precise FEF targeting in those participants). To explore this possibility, we fitted a second-  
 446 order polynomial function predicting the magnitude of the effect reported in the previous analysis  
 447 ( $\Delta$ ; i.e., the RT-difference between FEF and sham stimulation in the distractor-present conditions)  
 448 from the distance between FEF and M1 ( $d$ ) and on its square (i.e.,  $\Delta = \beta_0 + \beta_1 d + \beta_2 d^2 + \varepsilon$ ). The  
 449 squared term was included because we expected the distribution of the actual individual FEF-M1  
 450 distances to include both smaller and larger values with respect to the putative optimal distance  
 451 (Müri et al., 1991; Ro et al., 1999), such that the expected relationship between those values and  
 452 the strength of the measured behavioral effects might not be accommodated for by a linear trend  
 453 only. Interestingly, not only the analysis revealed a significant linear relationship ( $\beta_1 = -.42$ ;  $p =$   
 454  $.01$ ), indicating that the effect linearly decreased with the distance, but also a significant quadratic  
 455 effect ( $\beta_2 = .074$ ;  $p = .006$ ). These results imply that the effect of TMS was the strongest when  
 456 the distance between the putative right FEF stimulation site and the right M1 site was around 2.77  
 457 cm and decreased for both shorter and longer distances. This observation indicates that when the  
 458 putative FEF site, localized by means of neuro-navigation, was located anteriorly within a certain  
 459 anatomical distance from M1 (i.e., around 2-3 cm), the behavioral effects of right FEF stimulation  
 460 on distractor suppression were strongest, possibly indicating a more precise targeting of the actual  
 461 FEF location. This finding suggests that the localization of FEF relative to its distance from M1 (2-3  
 462 cm anterior) might provide a better strategy to target this brain area in future studies. As a  
 463 control, we performed the same analysis on the left hemisphere. Therefore, we fitted an  
 464 analogous second-order polynomial function predicting the magnitude of the effect (i.e., the  
 465 difference in RT between FEF and sham in the distractor-present conditions) from the distance

466 between left FEF and M1. This analysis did not reveal any significant effect ( $\beta_1 = -.13; p = .42;$   
 467  $\beta_2 = .026; p = .34$ ). (see Fig. 3D).

468

469 [Insert Fig. 3 about here]

470

471 Finally, given the significant impact of right FEF stimulation on distractor suppression, we  
 472 were also interested in testing whether these effects interacted with the recent trial history. To  
 473 this aim, log-transformed RTs were analyzed with a mixed linear model that included TMS (sham  
 474 vs. FEF), Distractor presence (present vs. absent) and Type of previous trial (distractor-present vs.  
 475 distractor-absent) as fixed-effect factors and intercept, TMS, Distractor presence and Type of  
 476 previous trial as random-effect coefficients across participants. As noted above, for this specific  
 477 analysis trials following incorrect-response trials were removed in addition to incorrect-response  
 478 trials. This analysis revealed a significant main effect of Distractor presence,  $F(1,28.5) = 189.92, p <$   
 479  $.001, (f^2_m = .060, f^2_c = .12)$ . As expected, the analysis confirmed that TMS modulated distractor  
 480 filtering by unveiling a significant interaction between TMS and Distractor presence,  $F(1,7394.0) =$   
 481  $13.07, p < .001, (f^2_m = .0008, f^2_c = .001)$ . The interaction between Distractor presence by Type of  
 482 previous trial revealed a trend towards significance,  $F(1,7398.9) = 3.04, p = .081$ . Interestingly, the  
 483 three-way interaction TMS by Distractor presence by Type of previous trial was nearly significant,  
 484  $F(1,7403.6) = 3.55, p = .059, (f^2_m = .001, f^2_c = .001)$ . In order to further explore this quasi-significant  
 485 interaction, we conducted separate analyses based on the Type of previous trial (distractor-absent  
 486 or distractor-present). When a distractor was present in the previous trial, no significant effect of  
 487 FEF TMS on the distractor cost was found, TMS by Distractor presence:  $F(1, 3602.3) = 1.71, p = .19$ .  
 488 Conversely, when a distractor was absent in the previous trial, TMS significantly modulated the  
 489 cost of distraction,  $F(1, 3743.2) = 15.05, p < .001, (f^2_m = .001, f^2_c = .003)$  (see Fig. 4). All of the other

490 effects or interactions did not reach significance (all  $ps > .081$ ). As a control, a similar analysis was  
 491 also performed comparing sham vs. right IPS stimulation. This analysis indicated a main effect of  
 492 Distractor presence,  $F(1, 28.6) = 196.58$ ,  $p < .001$ , ( $f^2_m = .069$ ,  $f^2_c = .13$ ) and a significant interaction  
 493 Distractor presence by Type of previous trial,  $F(1, 7433.2) = 7.19$ ,  $p = .007$ , ( $f^2_m = .0004$ ,  $f^2_c = .0008$ ).

494 For the right IPS stimulation condition, a non-significant effect was found for the  
 495 interaction TMS by Type of previous trial,  $F(1, 7432.4) < 1$ ,  $p = .39$ , albeit a marginally significant  
 496 effect was obtained for the interaction TMS by Distractor presence  $F(1, 7424.1) = 3.10$ ,  $p = .07$ . The  
 497 three-way interaction TMS by Distractor presence by Type of previous trial was non-significant,  
 498  $F(1, 7435.9) < 1$ ,  $p = .32$ . All of the other effects or interactions did not reach the significance level  
 499 (all  $ps > .08$ ).

500 [Insert Fig. 4 about here]

501

## 502 DISCUSSION

503 This study sought to ascertain the causal role of two key regions of the dorsal attention network,  
 504 FEF and IPS, in modulating attentional capture elicited by salient distractor stimuli. Results show  
 505 that TMS stimulation of the right FEF significantly reduced the behavioral interference caused by a  
 506 salient singleton distractor during a visual search task. Crucially, this was reliably different from  
 507 what observed following left FEF stimulation, which had no measurable effect on attentional  
 508 capture compared to a suitable sham condition. The magnitude of the reduction in distractor  
 509 interference associated with right FEF stimulation correlated with the anatomical distance  
 510 between the putative FEF stimulation site and M1 at the single-subject level and peaked in  
 511 participants for whom such distance was between 2-3 cm, compatible with functional localization  
 512 evidence (Ro et al., 1999). Interestingly, an additional analysis attributed reduction in distractor

513 costs following right FEF stimulation to performance improvements occurring in the distractor-  
 514 present condition, which attests to the specificity of our results. Perhaps even more interestingly,  
 515 further analyses indicated that this lessening of distractor costs interacted with modulations of  
 516 distractor interference due to inter-trial contingencies. In particular, the reduction of distractor  
 517 interference observed during right FEF stimulation was maximized when the previous trial was a  
 518 distractor-absent vs. distractor-present trial. Taken together, these results attest to the pivotal  
 519 role of the right FEF in both limiting attentional capture by salient distractors and modulating  
 520 history-contingent distractor interference.

521 Our main result reveals a causal role of right FEF in on-line distractor filtering. This result  
 522 aligns nicely with the general idea that the human prefrontal cortex is responsible for controlling  
 523 and filtering task-irrelevant information (de Fockert et al., 2004; de Fockert & Theeuwes, 2012;  
 524 Geng, 2014; Kane & Engle, 2002; Marini et al., 2016; Shimamura, 2000). A recent brain stimulation  
 525 study showed that tDCS stimulation over bilateral prefrontal cortex led to a decrease in  
 526 attentional capture in the additional singleton task (Cosman et al., 2015). Additional evidence that  
 527 prefrontal regions directly drive the efficient filtering of irrelevant information comes from event-  
 528 related potentials (ERPs) studies, which identified a frontal ERP component presumably related to  
 529 distractor suppression (the *frontal bias signal*; Liesefeld, Liesefeld, & Zimmer, 2014; Vissers, van  
 530 Driel, & Slagter, 2016; Vogel, McCollough, & Machizawa, 2005). Several functional magnetic  
 531 resonance imaging (fMRI) studies have also provided converging evidence on the role of prefrontal  
 532 cortex in filtering-out irrelevant stimuli. For example, brain activity levels in the prefrontal cortex  
 533 correlated with the magnitude of the interfering effects engendered by salient distractors as  
 534 measured behaviorally (de Fockert et al., 2004; de Fockert & Theeuwes, 2012; Leber, 2010). More  
 535 relevant for the interpretation of the current results, a brain-behavior relationship has been  
 536 established between activity levels in the right prefrontal cortex (right inferior frontal gyrus, rIFG,



537 and right middle frontal gyrus, rMFG) and behavioral indexes of distractor suppression (Demeter  
538 et al., 2011; Marini et al., 2016; Weissman et al., 2006). The distinctive role of a right-lateralized  
539 network in attentional control has also been confirmed by neuropsychological evidence, pointing  
540 to the rMFG as a crucial node for regulating both top-down and bottom-up attention (see Japee,  
541 Holiday, Satyshur, Mukai, & Ungerleider, 2015). In the present study, the delivery of repetitive  
542 TMS immediately after target (and distractor) presentation may have modulated ongoing activity  
543 by increasing neuronal excitability within a network of right-lateralized prefrontal attentional  
544 control regions (including rIFG, rMFG and rFEF). This may have rendered the network prompter to  
545 process upcoming visual stimuli, in turn resulting in an optimal instantiation of distraction-filtering  
546 mechanisms in the presence of a salient distractor. The existence of strong functional interactions  
547 between the FEF, which is part of the dorsal attention network, and the rMFG and rIFG, which are  
548 part of the ventral attention network, is supported by several resting-state connectivity studies  
549 (Asplund et al., 2010; Fox et al., 2006; He et al., 2007; Shulman et al., 2009). Crucially, DiQuattro  
550 and colleagues (DiQuattro & Geng, 2011; DiQuattro et al., 2014) reported that an excitatory  
551 pathway from the temporoparietal junction (TPJ) to IFG to FEF contributed to the optimal  
552 suppression of irrelevant yet salient distractors. The interpretation of the current results in terms  
553 of a facilitating role of TMS in the instantiation of distractor filtering mechanisms fits perfectly  
554 with very recent findings in the macaque, demonstrating a shared neural substrate for target  
555 selection and distractor suppression in FEF neuronal populations (Cosman et al., 2018). More  
556 specifically, this study demonstrated that signatures of (target selection and) salient-distractor  
557 filtering in FEF neurons preceded by ~50 ms posterior ERP signatures of the same process, likely  
558 reflecting proactive suppression of the salient distracting stimulus before it can affect neural  
559 selection and eventually capture attention (see also Gaspelin et al., 2015; Gaspelin & Luck, 2018;  
560 Sawaki & Luck, 2010). In this framework, it is possible that ERPs markers of attentional

561 suppression reported in human participants (A. M. Liesefeld et al., 2014; H. R. Liesefeld et al.,  
 562 2017) reflect the successful control against distraction which is implemented by pre-frontal cortex  
 563 circuitry (and in particular right FEF). This would support the general notion that prefrontal-  
 564 extrastriate projections are responsible for both enhancing task-relevant information and  
 565 suppressing irrelevant, and especially distracting, information (Cosman et al., 2018; Gazzaley et al.,  
 566 2007; Ruff & Driver, 2006; Serences et al., 2004).

567       Our results are compatible with the idea that TMS facilitated the instantiation of distractor  
 568 suppression. An alternative interpretation is that the right FEF stimulation may have disrupted the  
 569 attentional bias towards the salient visual feature (the odd color), since this might also lead to  
 570 reduced capture by the salient distractor. Indeed, it is well known that both FEF and IPS are  
 571 involved in attentional capture and salience-dependent computations (Corbetta & Shulman, 2002;  
 572 Serences et al., 2005). Electrophysiological studies with non-human primates have consistently  
 573 demonstrated that visual saliency maps are represented in multiple fronto-parietal regions,  
 574 including LIP (Gottlieb et al., 1998) and FEF (Schall & Hanes, 1993), as well as in subcortical  
 575 structures, notably the superior colliculus (see White et al., 2017). In the present experiment, TMS  
 576 may have interfered with attentional mechanisms that are responsible for biasing attention  
 577 towards salient items. This, in turn, may have weakened attentional capture and reduced the RT-  
 578 cost engendered by salient distractors. In principle, a similar argument could be made for IPS  
 579 stimulation, which, however, did not significantly modulate the behavioral cost produced by  
 580 salient distractors. Possibly, the contribution of FEF to attentional biasing towards salient stimuli  
 581 may be either stronger or more susceptible to TMS-induced modulations than that of IPS.  
 582 Incidentally, the early involvement of pre-frontal regions in bottom-up attention, as shown by  
 583 research on non-human primates, suggests that the identification of salient visual stimuli in  
 584 parietal and frontal regions may proceed in parallel rather than serially (Katsuki & Constantinidis,

2012; Thomas & Paré, 2007; Thompson et al., 1996). Although the occurrence of a TMS-induced deficit in saliency computation may seem compatible with the available evidence, for at least two reasons we consider this possibility less likely than our previous interpretation in terms of distraction-filtering mechanisms. First, if saliency computation were compromised by the right FEF TMS stimulation, then we might expect a performance cost in the distractor-absent condition too, since saliency computation should have also supported target selection, in addition to attentional capture by the singleton distractor. However, our data indicated no TMS-induced modulation of performance in the distractor-absent condition. Second, an interpretation in terms of saliency computation does not seem to provide an obvious account for the effects of TMS on modulations of performance related to cross-trial contingencies (see below). For these reasons, we favor an interpretation whereby right FEF TMS modulated mechanisms responsible for the effective filtering of salient distractors.

The negative results we found for the IPS stimulation may appear at odds with those reported by Hodsoll and colleagues (2009), as they described a significant reduction in the distractor cost following right PPC TMS. However, crucial differences in the TMS protocol may account for the discrepant results. Hodsoll and colleagues used an off-line, 1 Hz TMS approach, known to give rise to prolonged cortical inhibition at the site of stimulation (Chen et al., 1997; Oliveri et al., 2005). Instead, our time-locked, 10 Hz stimulation protocol may have been suboptimal for inducing clear-cut behavioral changes following IPS stimulation. In line with this interpretation, previous ERP studies demonstrated a sequential involvement of FEF and IPS during distractor-filtering tasks, with frontal signals preceding those detected over parietal areas (Brignani et al., 2009; Grent-‘t-Jong & Woldorff, 2007; Leblanc et al., 2008; A. M. Liesefeld et al., 2014; Ptak et al., 2011; Shomstein et al., 2012). Therefore, we cannot exclude the possibility that the early stimulation (between 100-300 ms after display onset) applied in the current study was

adequate for affecting FEF but not IPS activity, and that a later or more prolonged stimulation may reveal the involvement of IPS in the current behavioral context. These remain open possibilities for future studies to explore.

The present results are also compatible with the proposed general role of the fronto-parietal attention network in modulating the responsiveness of visual cortical regions (Baluch & Itti, 2011; Bisley & Goldberg, 2010; Buschman & Kastner, 2015; Grosbras & Paus, 2003; Marini et al., 2016; Moore & Armstrong, 2003; Noudoost et al., 2010; Scolari et al., 2015; Silvanto et al., 2006, 2009). The available evidence suggests that suppression mechanisms may be implemented through prefrontal-driven modulations of sensory processing (Gazzaley et al., 2007; Seidl et al., 2012; Serences et al., 2004), similarly to sensory enhancements of target features (Chelazzi et al., 2011; Reynolds & Chelazzi, 2004). Moreover, recent findings both in humans (Michalareas et al., 2016; Popov et al., 2017; C. Wang et al., 2016) and non-human primates (Bastos et al., 2015; van Kerkoerle et al., 2014) suggest that FEF may exert top-down control by modulating visual oscillatory alpha-band activity in sensory areas. Recently, Popov et al. (2017) used magnetoencephalography (MEG) to show that right FEF, but not left FEF, exerts top-down control on stimulus processing in visual cortex. This FEF hemispheric asymmetry fits well with our current results and is complemented by the typical finding that TMS modulates visual task performance in both (left and right) hemifields when applied over the right FEF, and in the right hemifield only when applied over the left FEF (Grosbras & Paus, 2003; Silvanto et al., 2006; Smith et al., 2005). In general, the present results concur with the large body of evidence suggesting a right hemispheric dominance for the control of visuo-spatial attention in the FEF (Capotosto et al., 2009; Duecker et al., 2013; Grosbras & Paus, 2003; Marshall et al., 2015; Silvanto et al., 2006; C. Wang et al., 2016).

Interestingly, the beneficial effects of right FEF stimulation on distractor suppression seem to interact with modulations of distractor costs that are related to the presence vs. absence of a

distractor in the preceding trial, suggesting a role of the right frontal attention network in the inter-trial, history-dependent regulation of distraction-filtering mechanisms. More specifically, in the sham condition, the interfering effect of the distractor was greater on trials following a distractor-absent trial compared to trials following a distractor-present trial – an observation that has been reported previously (Geyer et al., 2008). The TMS stimulation of right FEF eliminated the relative disadvantage of having experienced a distractor-absent condition in the previous trial, which could be alternatively interpreted as if TMS mimicked the advantage of having encountered a distractor-present condition. We have already suggested that the effect of TMS on neuronal excitability might have consisted of an increase of activity in neuronal populations implementing distractor-filtering mechanisms in the current trial. In addition, TMS may have also facilitated the sustained maintenance of distraction-filtering mechanisms through the subsequent trial, hence resulting in a reduction of the distractor cost. This idea can be accommodated in the framework of the interactions between the conflict monitoring system (Botvinick et al., 2001) and the fronto-parietal attention network. According to this framework, when response conflict occurs, the anterior cingulate cortex (ACC) signals an increased demand for cognitive control, which leads to an enhancement of top-down control mediated by the dorsal fronto-parietal network (FEF and IPS; see Walsh et al., 2011) on the subsequent trial (Botvinick et al., 2001; Carter et al., 2000; Casey et al., 2000). From an anatomical and physiological perspective, this is supported by the existence of direct axonal projections between ACC and both FEF (Huerta et al., 1987; Stanton et al., 1993) and PPC (Hampson et al., 2006; Pandya et al., 1981). Perhaps similarly to response conflict, also the presence of a salient distractor may trigger the ACC reactively (see Seeley et al., 2007) and then engage greater attentional control proactively in preparation for the subsequent trial, thus leading to reduced distractor costs. Here, magnetic stimulation may have primed the attention control network in a way that mimicked the proactive adjustments occurring

657 spontaneously after distractor-present trials. This, in turn, would have resulted in a reduced  
 658 distractor cost in the subsequent trial. The idea that right FEF TMS may have promoted proactive  
 659 trial-to-trial control finds support in a study by Leber (2010) showing that stronger pre-trial activity  
 660 in prefrontal areas was associated with reduced distractor interference by a salient irrelevant  
 661 distractor.

662         As a cautionary note, the design of our experiment is not optimally suited to draw firm  
 663 conclusions concerning the effect of TMS on inter-trial modulations. Indeed, by applying TMS  
 664 pulses on every trial, we cannot cleanly disentangle whether the reported effects were due to an  
 665 influence of TMS on the current trial (N) or instead on the previous trial (N-1). Regardless of this  
 666 limitation, our results demonstrated that following right FEF stimulation the relative disadvantage  
 667 of having experienced a distractor-absent condition in the previous trial was completely  
 668 eliminated. This finding can be interpreted in two alternative ways: On the one hand, TMS on the  
 669 current trial N may have strengthened reactive (on-line) mechanisms to deal with distraction,  
 670 those very mechanisms that are especially important when the system has not been alerted by a  
 671 distractor on the preceding trial. Alternatively, TMS on the previous (distractor-absent) trial may  
 672 have proactively primed the attention control network, mimicking the modulation occurring  
 673 spontaneously on distractor-present trials. Future and more sensitive TMS experimental designs  
 674 will help clarify this distinction.

675         In conclusion, with a systematic approach, the present findings indicate a causal role of the  
 676 right FEF in adjusting attentional filtering mechanisms. We propose that the TMS intervention  
 677 engaged the cortical network that controls and regulates mechanisms for limiting interference  
 678 from irrelevant, attention-capturing distractor stimuli. More specifically, TMS may have shielded  
 679 the network from the impact of potential distractor interference, both by facilitating on-line  
 680 distractor filtering mechanisms and by modulating inter-trial adjustments. Moreover, our results

681 suggest that not only right FEF is directly involved in the reactive control mechanisms that deal  
682 with distracting stimuli after their appearance, but it also mediates attentional control  
683 mechanisms that are modulated on a trial-by-trial basis. Future research will have to elucidate the  
684 contribution to distraction filtering of other cortical regions, notably ventral attention network  
685 regions such as IFG/MFG in the frontal lobe and TPJ in the parietal lobe, and will clarify whether  
686 the role of ventral regions is similar or distinguishable from the role of the dorsal attention  
687 network characterized here.

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## FIGURE LEGENDS

**Fig.1.** Experimental procedure. **A.** Representation of the four possible types of search arrays used in the task. In 50% of trials all display items were of the same color (e.g., red; distractor-absent condition), whereas in the remaining 50% of trials three items were of the same color (e.g., red) and the fourth item (additional singleton) was of the alternative color (e.g., green; distractor-present condition). The target, indicated with a dashed circle for graphical purposes only, was defined as the unique double-arrowhead item. **B.** Timeline of an experimental trial (see text for a detailed description). Three TMS pulses were delivered at 10 Hz (pulse gap of 100 ms) starting 100 ms after search array onset. **C.** Schematic representation of the stimulated sites: Talairach coordinates were  $x=-36, y=-1, z=48$  and  $x=36, y=-1, z=48$  for left and right FEF, respectively, and  $x=-30, y=-53, z=49$  and  $x=30, y=-53, z=49$  for left and right IPS, respectively (red circles). The two sham conditions (white circles) were in a region on the scalp located halfway between IPS and FEF of the left and right hemisphere, respectively.

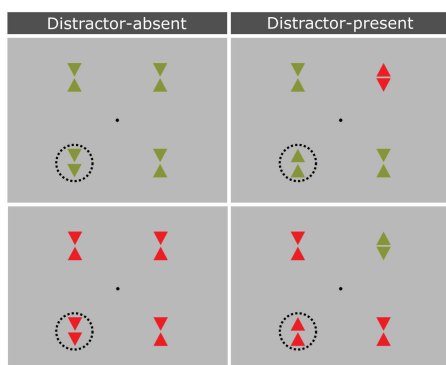
**Fig.2.** Behavioral effects calculated in the sham condition. **A-B.** Mean RTs (A) and mean accuracy (B) for trials with a singleton distractor relative to trials without. **C-D.** Difference RTs (C) and difference accuracy (D) for trials in which the singleton distractor was present relative to absent (distractor cost), shown as a function of the type of previous trial (distractor-present vs. distractor-absent). Error bars represent  $\pm 1$  SEM. ( $***p < 0.001$ ,  $**p < 0.01$ ,  $*p < 0.05$ ).

**Fig.3.** TMS effects on visual search. **A.** Difference RTs for trials in which there was a singleton distractor relative to trials in which it was absent (distractor cost), shown as a function of the TMS site (sham, FEF and IPS) and brain hemisphere (left, right). The effect of right FEF stimulation was

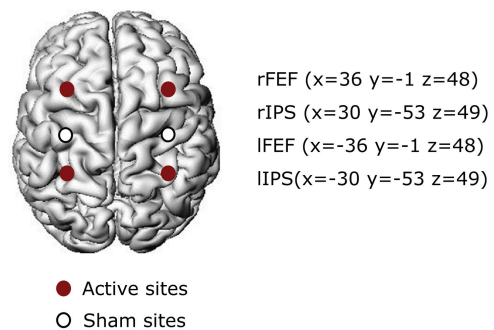
significantly different relative to left FEF stimulation: The distractor cost was significantly reduced after right FEF stimulation compared to its correspondent sham control condition. Error bars represent  $\pm 1$  SEM. ( $**p < 0.01$ ). **B.** Mean RTs for the distractor-present condition, as a function of TMS site and brain hemisphere. Error bars represent  $\pm 1$  SEM. ( $*p < 0.05$ , Bonferroni-Holm corrected). TMS over right FEF significantly reduced RTs compared to the corresponding right sham control condition. **C.** Mean RTs for the distractor-absent condition, as a function of TMS site and brain hemisphere. Error bars represent  $\pm 1$  SEM. **D.** Quadratic regression predicting the magnitude of the significant effect (i.e., RT-difference between FEF and sham in the distractor-present condition) after the distance between putative FEF and M1 in individual participants, separately for each hemisphere. The effect of TMS was the strongest when the distance between right putative FEF and right M1 was around 2.77 cm. The shaded area represents the 95% confidence interval of the best-fit line.

**Fig.4.** Difference RTs for trials in which the singleton distractor was present minus absent, shown as a function of the type of previous trial (distractor-absent vs. distractor-present). Data are shown for sham vs. FEF stimulation on the right hemisphere. The relative RT-disadvantage following distractor-absent vs. distractor-present trials decreased following FEF stimulation compared to sham. Error bars represent  $\pm 1$  SEM. ( $***p < 0.001$ ).

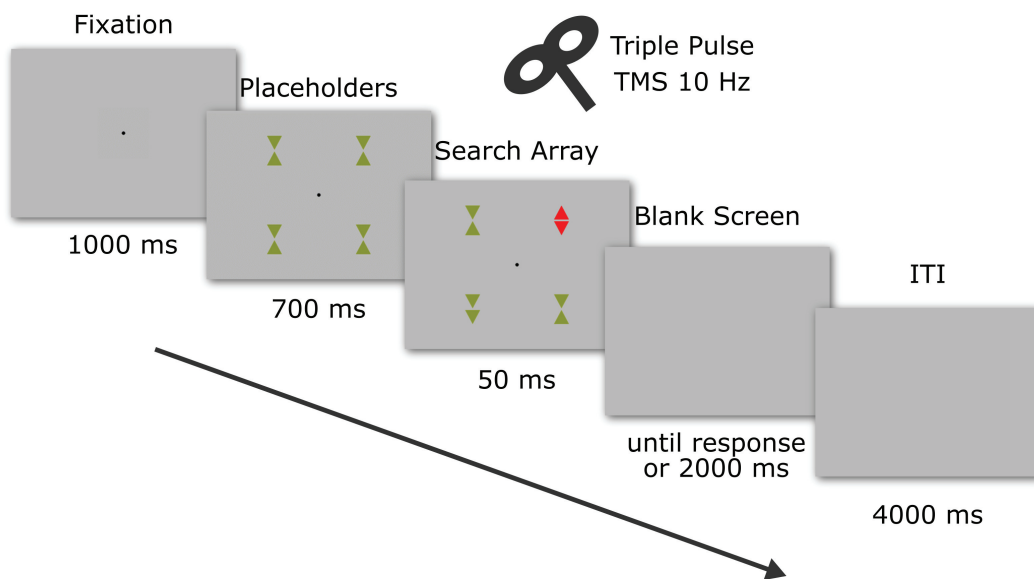
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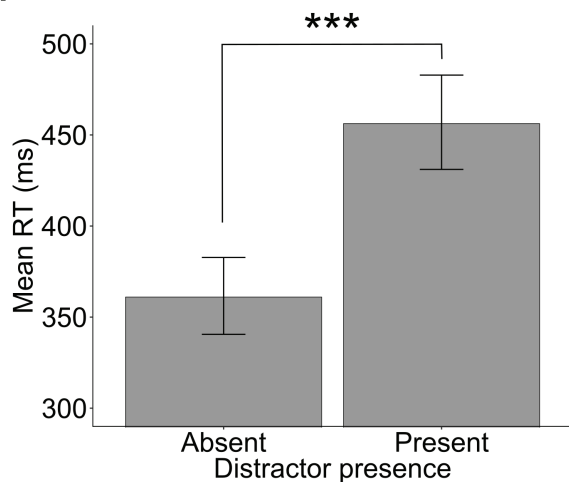
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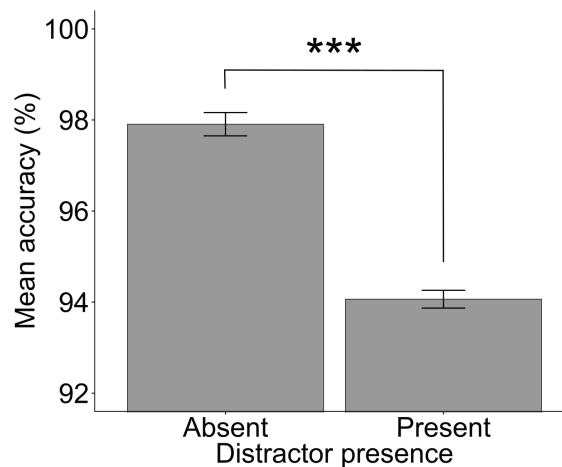
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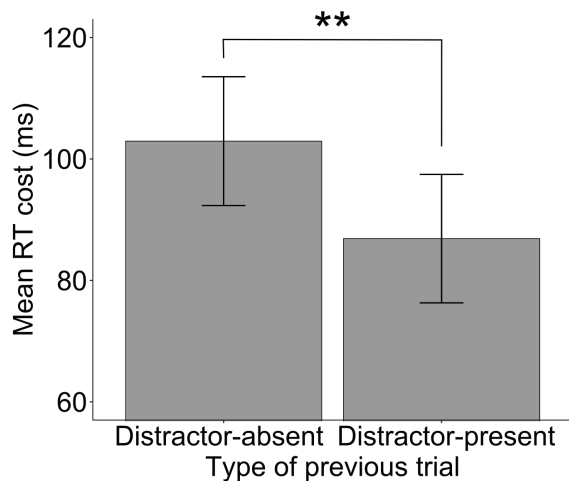
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B



C



D

