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TMS on Right Frontal Eye Fields Induces an Inflexible Focus of Attention

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The focus of spatial attention can be not only oriented to a particular location, but also adjusted in its size to select visual information from a narrow (zoom-in) or broad (zoom-out) region of the visual field. Attentional orienting, saccades programming, and visual search have been linked to the frontal eye fields (FEF) activity. However, the FEF causal role in the frontoparietal network for the attentional focus size modulation remains unclear. Here, we delivered single-pulse transcranial magnetic stimulation (TMS) on FEF while participants performed an attentional zooming task. They were asked to detect a visual target appearing at 3 eccentricities from the fixation. Two cue types modulated the size of the attended region: a small cue was employed to narrow the attentional focus, whereas a large cue induced participants to broaden the attended region. Results showed that TMS delivered on the right FEF, but not on the left FEF, was able to interfere with both zoom-in and zoom-out attentional mechanisms. Our results provide the first evidence of the right FEF casual role in the attentional zooming control and give new insights into the neural mechanisms of dysfunctional spatial attention deployment shown in neurodevelopmental disorders, such as autism and dyslexia.

Keywords: attentional scaling, frontal cortex, pervasive developmental disorder, reading disorder, visual attention

Introduction

The selection of relevant visual information is controlled by spatial attention. The focus of attention can be moved to a particular region in the visual space, also in absence of eye movements (i.e., covert orienting of attention; Posner, 1980). Moreover, the focus of attention can be adjusted in its size, like a "zoom-lens" (e.g., Eriksen and St James 1986; Castiello and Umiltà 1990; Greenwood and Parasuraman 1999), to be spread in a broader portion (zoom-out) or focused in a narrow region (zoom-in) of the visual field. Neuroimaging and neurophysiological data supported this hypothesis, suggesting that the neural activity preceding the target presentation was finely modulated by the attended region in early visual areas (Vidyasagar 1998; Brefczynski and DeYoe 1999; Müller et al. 2003; McAdams and Reid 2005; Ruzzoli et al. 2011), and that the attentional zooming modulated both P1 and N1 components of the visual event-related potentials (Luo et al. 2001; Fu et al. 2005).

It is widely demonstrated that a frontoparietal network, composed of superior frontal cortex (in particular, frontal eyes fields, FEF) and intraparietal sulcus, plays a crucial role on covert orienting of attention (see Corbetta and Shulman 2002, 2011 for reviews). However, the brain areas devoted to control the attentional focus size have not been specifically investigated yet. In particular, there is no evidence regarding the role of FEF. The predominant view of visual cognition associated FEF with eye movement programming (see Tehovnik et al. 2000 for a review). The hypothesis of a strict link between covert spatial attention and eye movement programming was originally suggested by Rizzolatti et al. (1987). After this proposal, the role of FEF has been increasingly recognized to go beyond the programming of eye movements. Previous studies showed that the FEF area of the macaques was involved in visual target selection during a visual search task (e.g., Bichot and Schall, 1999; Murthy et al. 2001). Further evidence came from transcranial magnetic stimulation (TMS) studies in human participants, which demonstrated the FEF fundamental role in covert orienting of attention (e.g., Ro et al. 2003; Taylor et al. 2007) and in serial visual search (see O'Shea et al. 2006 for a review). Importantly, recent concurrent TMS and functional neuroimaging studies suggest the casual role for FEF in the frontoparietal modulation of neural activity in both striate and extrastriate visual areas (Ruff et al. 2006, 2009).

The aim of the present study was to investigate the role of FEF in the modulation of the attentional focus size. Single-pulse TMS was used to interfere with cue processing of a cue that induced subjects to narrow or to broaden the attentional focus. We measured simple reaction times (RTs) to a visual target that could appear at 1 of 3 eccentricities from the fixation. We used the term "attentional gradient" to indicate the specific RTs pattern, dependent on target eccentricity, that is influenced by the 2 different cue sizes employed (LaBerge 1983; see LaBerge and Brown 1989 for a review). When a small cue (containing only the first target eccentricity) preceded the target onset, subjects are induced to zoom-in their focus of attention, generating a significant attentional gradient (i.e., increasing RTs with increasing target eccentricity). On the other hand, when a large cue (containing all possible target eccentricity) anticipated the target onset, subjects automatically zoom-out their attentional focus to cover all the possible target locations. Consequently, the attentional gradient is usually reduced or even nullify (equal RTs across eccentricities) in presence of a large cue. This prediction should be valid only within a limited cue-target time window, as suggested by previous studies that investigated the specific time course of the attentional focusing (e.g., Benso et al. 1998; Turatto et al. 2000; Ronconi, Gori, Ruffino, Molteni et al. 2012; Ronconi, Gori, Ruffino, Franceschini et al. 2012). In particular, Turatto et al. (2000) provided evidence of automatic and voluntary attentional mechanisms controlling the size of the focus. When a new object suddenly appears in the visual field, the focus automatically adjusted its size. Accordingly, Benso et al. (1998) showed that the focusing mechanism takes between 33 and 66 ms to be initiated but for long SOAs, the focus collapses.

As it is a widely held view that the right hemisphere is dominant for spatial attention (Corbetta and Shulman 2002, 2011), our prediction is that only TMS of the right FEF would interfere with the attentional zoom-lens control.

Materials and Methods

Participants

Fifteen adult participants (age range 22–27 years, mean age = 24.33 years, all right-handed) without any history of neurological or psychiatric disorder took part in the present study as paid volunteers. Six participants took part in the "No TMS experiment" (Experiment 1), while the other 9 participants performed the "TMS experiment" (Experiment 2). All had normal or corrected to normal vision and provided informed consent before participation. The entire research protocol was conducted in accordance to the principles elucidated in the Declaration of Helsinki and the ethical committee of the Department of General Psychology of the University of Padua approved the study.

Apparatus and Procedure

No TMS Experiment (Experiment 1)

The experiment was conducted in a dimly lit and quiet room. Participants were seated 40 cm away from a 19-inch CRT monitor. A chinrest was used to stabilize the head; fixation was binocular. All stimuli were middle gray displayed on a black background. The fixation point was a cross of 0.5° placed in the screen center. One circle was presented concentrically to the fixation point, and the dimension of its ray was manipulated according to the 2 cue conditions: 4° in the small and 12.5° in the large cue condition (Fig. 1). The target stimulus was a dot of 0.5°, which could appear at 1 of 3 possible horizontal eccentricity (i.e., 2, 6, and 12°, namely: Eccentricities 1, 2, and 3, respectively). In the small cue condition, the target was displayed inside the focusing cue at Eccentricity 1, whereas at Eccentricity 2 and 3, it felt outside. In the large cue condition, the target was always displayed inside the focusing cue. The target was randomly presented either in the left or in the right visual hemifield. Similar experimental paradigms have already been employed in other studies (Facoetti and Molteni 2001; Ronconi, Gori, Ruffino, Molteni et al. 2012; Ronconi, Gori, Ruffino, Franceschini et al. 2012).

At the beginning of each trial, a central fixation point appeared for 1000 ms. Subsequently, a noninformative small or large cue was presented (i.e., the probability of the target location was equal in the 2 focusing cue conditions). After a variable stimulus onset asynchrony (SOA: 100, 300, or 500 ms), the target was displayed for 20 ms. A short target duration was chosen to prevent eye movements after the stimulus onset. Participants were instructed to press the space bar with their right hand as fast as possible at the target onset. If no response was provided within 1000 ms from the stimulus onset, participants were warned with a 800-Hz sound played for 500 ms. At the end of each trial, a blank screen for an intertrial interval of 1500 ms was presented before starting the following trial. The entire experiment consisted of 1440 trials, run in 2 separate sessions of 720 trials, with a few hours of break between them. Both sessions were identical, and consisted in 3 different blocks of 240 trials. Each block contained 216 response trials (108 trials for the 2 focusing cue sizes; 36 trials for each target location) and 24 catch trials (target absent).

TMS Experiment (Experiment 2)

Experiment 2 used the same behavioral procedure of Experiment 1, but TMS stimulation was included. Single-pulse TMS was performed using a Magstim Rapid² stimulator and a 70-mm figure 8-shaped coil (The Magstim Company, Ltd.) combined with the Brainsight frameless stereotactic navigation system (Rogue Research Inc., Montreal, Canada).

Single-pulse TMS was delivered on the right FEF (r-FEF, experimental condition) and on the left FEF (l-FEF, control condition). The stimulation was time-locked to each trial, either 0 or 70 ms after the cue onset, and randomized across trials. We separated the 2 stimulation sites (r-FEF and l-FEF) into different blocks. The same

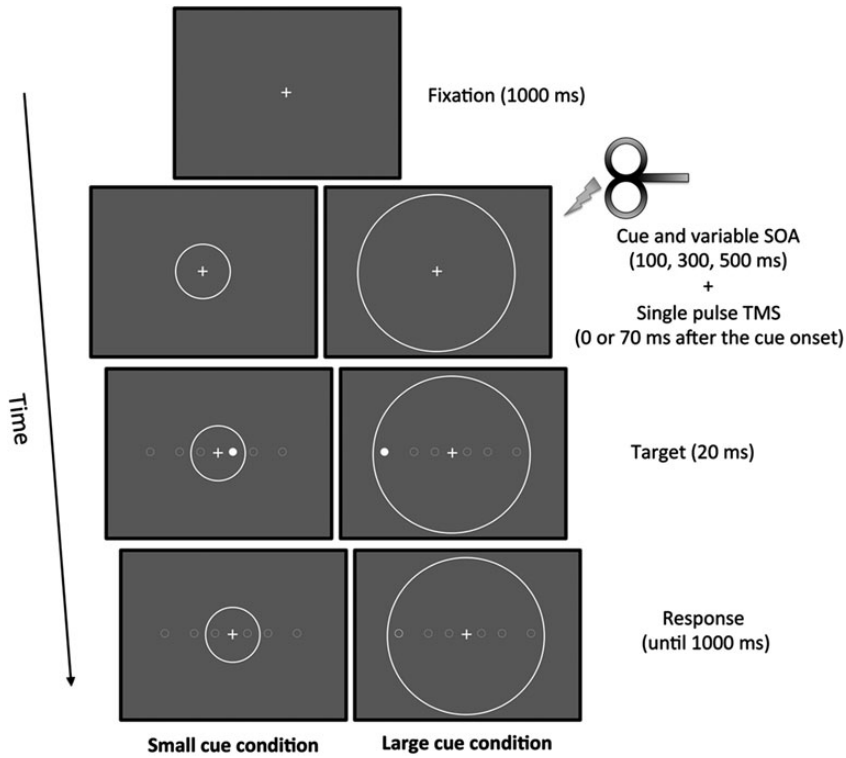

Figure 1. Schematic illustration of the task design (SOAs, stimulus onset asynchronies; TMS, transcranial magnetic stimulation). Target appeared randomly in 1 of the 6 positions depicted along the horizontal axis (not shown while participants performed the task).

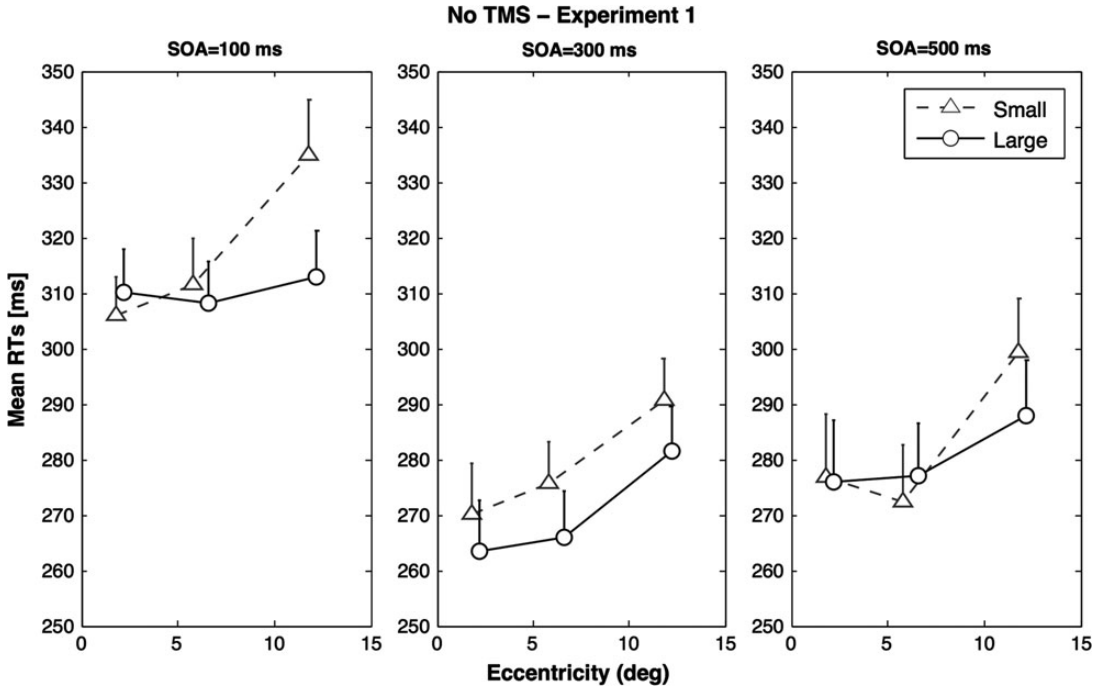

Figure 2. Results of the behavioral experiment (Experiment 1), showing mean RTs as a function of the Cue (small vs. large), Eccentricity (2, 6, and 12°) and stimulus onset asynchronies (SOAs: 100, 300, and 500 ms). Error bars represent the SEM.

administration order was repeated for the 2 sessions and was randomly counterbalanced across participants.

The r-FEF and the control (l-FEF) sites were localized moving the coil 3 cm rostrally from each subject's motor hotspots and 5 cm laterally of the sagittal midline. These positions were then marked with the Brainsight software. The handle of the coil was oriented posteriorly. The precise location of the FEFs varies from individual to individual (Ro et al. 2002), and this could be a possible source of error. However, the same procedure has been successfully employed in previous TMS studies (e.g., Müri et al. 1991; Ro et al. 1999; Leff et al. 2001; O'Shea et al. 2006). When participants reported discomfort caused by TMS-evoked blinks and facial twitches, the orientation of the coil was altered slightly, without any change in position. Stimulation was delivered at 100% of the motor threshold, considered as the minimal intensity necessary to elicit a visible movement of the hand in 5 of 10 stimulation pulses produced on the contralateral motor hotspot (mean intensity for the r-FEF was 51.22 ± 4.26; mean intensity for the l-FEF was 50.67 ± 4.47, $t_8 = 0.73$, $P > 0.05$).

Results

No TMS Experiment (Experiment 1)

Mean RTs for the correct response trials were used as the dependent variable for the 3-way repeated measures ANOVA with the following within subject factors: Cue (small and large), SOA (100, 300, and 500 ms) and Eccentricity (2, 6, and 12°). The main result is a significant cue × SOA × eccentricities interaction ($F_{4,20} = 2.91$, $P < 0.05$, $\eta_p^2 = 0.37$). This interaction showed the specific time course of the cue size effect on the RTs at the 3 eccentricities (Fig. 2). Planned comparisons at 100-ms SOA ($F_{2,10} = 20.37$, $P < 0.05$, $\eta_p^2 = 0.80$) showed that RTs difference between Eccentricity 1 and Eccentricity 3 was significant in the small cue condition (306 ms; SE = 7 and 335 ms; SE = 10 respectively; $F_{1,5} = 39.3$, $P < 0.05$, $\eta_p^2 = 0.89$), but not in the large cue condition (310 ms; SE = 8 and 313 ms; SE = 8 respectively; $F_{1,5} < 1$, $\eta_p^2 = 0.07$). In contrast, planned comparisons at the other SOAs did not reveal any significant cue × Eccentricity (SOA = 300 ms: $F_{1,5} < 1$, $\eta_p^2 = 0.04$; SOA = 500 ms: $F_{1,5} = 2.25$, n.s., $\eta_p^2 = 0.31$). These results show that an automatic control of the attentional focus is present only when the target appeared 100 ms after the cue.

The ANOVA revealed also a main effect of cue ($F_{1,5} = 18.17$, $P < 0.01$, $\eta_p^2 = 0.78$), SOA ($F_{2,10} = 23.49$, $p < 0.05$, $\eta_p^2 = 0.82$), and Eccentricity ($F_{2,10} = 37.28$, $P < 0.05$, $\eta_p^2 = 0.88$). No other main effect or interaction was significant.

The "Attentional Gradient" as a Measure of the Attentional Focus Modulation

According to the results of the Experiment 1, we calculated an Attentional Gradient (AG) index (Ronconi, Gori, Ruffino, Molteni et al. 2012; Ronconi, Gori, Ruffino, Franceschini et al. 2012) for the 100 ms SOA. The AG was obtained separately for the small and large cue conditions, subtracting the Eccentricity 1 from the Eccentricity 3 RTs. As can be seen from the Figure 4*A*, in the Experiment 1, the AG was significantly different between the large (mean AG = 2.62 ms, SE = 4) and the small cue condition (mean AG = 29.01 ms, SE = 5; $F_{1,5} = 37.52$, $P < 0.05$, $\eta_p^2 = 0.88$). This difference was not significant at the other SOAs (300 and 500 ms, all ps > 0.05). In the light of these results, we focused the analysis of the Experiment 2 on the AG calculated at the first SOA.

TMS Experiment (Experiment 2)

In Experiment 2, we used the raw RTs mean of the correct response trials (see Fig. 3) to compute the AG values mean, and performed a 3-way repeated measures ANOVA (2 × 2 × 2) with the following within subjects factors: Cue (small and large), Site (l-FEF and r-FEF), and TMS timing (0 and 70 ms from the cue onset). The main result is a significant cue ×

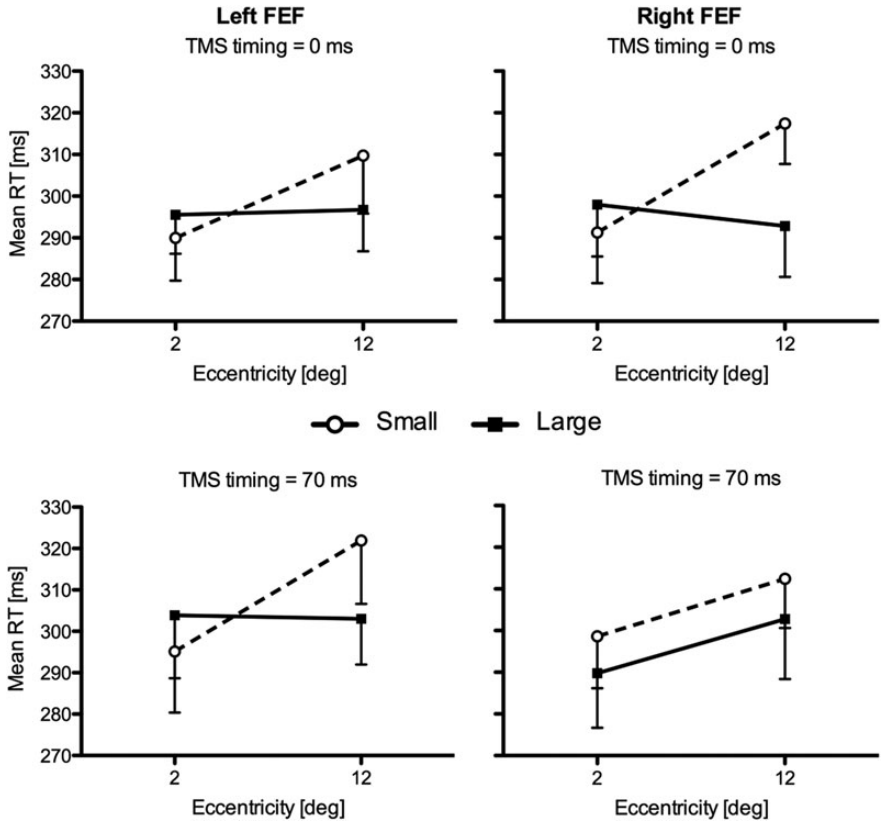

Figure 3. The mean raw RTs are depicted as a function of TMS sites (left FEF vs. right FEF), cue (small vs. large), and eccentricity (2 vs. 12°). Error bars represent the SEM.

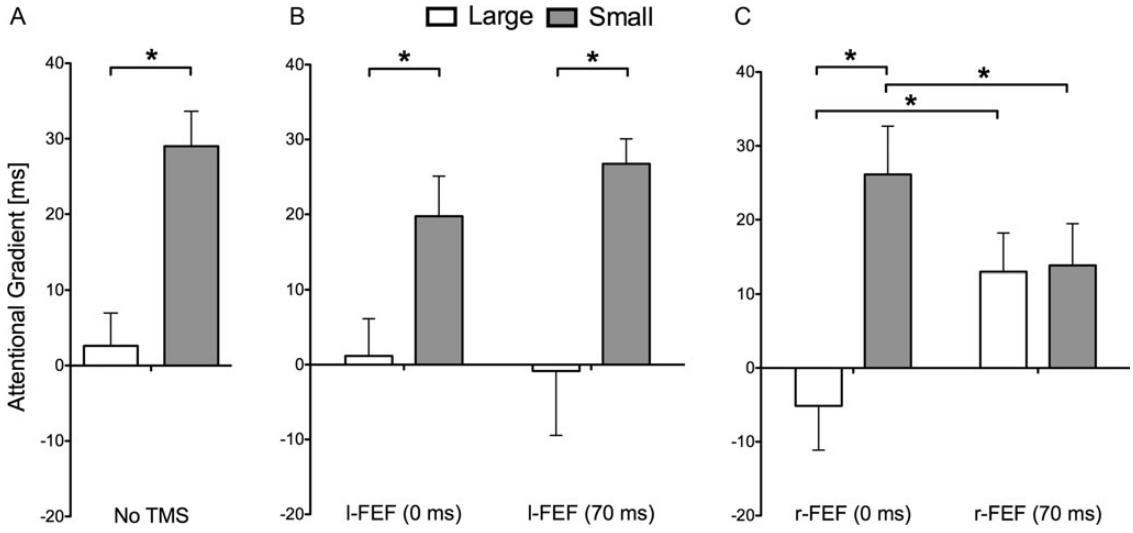

Figure 4. The mean attentional gradient (AG; i.e., difference between RTs at Eccentricity 3 [12°] and RTs at Eccentricity 1 [2°]) is depicted as a function of cue and TMS condition: (*A*) No TMS, (*B*) TMS on the left FEF (control site) and (*C*) TMS on the right FEF. Error bars represent the SEM. Asterisk indicates a significant difference as revealed by planned comparisons ($P < 0.05$).

site × TMS timing interaction ($F_{1,8} = 7.17$, $P < 0.05$, $\eta_p^2 = 0.47$; see Fig. 4*B*,*C*) which was explored by the following planned comparisons. For the l-FEF site (Fig. 4*B*), comparison revealed that the AG was significantly different between the small and the large cue condition, regardless of the TMS timing (0-ms TMS timing: mean AG = 1.17 ms for the large cue, SE = 5; mean AG = 19.75 ms for the small cue, SE = 5; $F_{1,8} = 12.78$, $P < 0.05$, $\eta_p^2 = 0.61$; 70-ms TMS timing: mean AG = −0.86 ms for the large cue, SE = 9; mean AG = 26.76 for the small cue, SE = 3; $F_{1,8} = 10.69$, $P < 0.05$, $\eta_p^2 = 0.57$). This result indicates

that participants automatically adjusted their focus of attention when the single-pulse TMS was delivered at the l-FEF site, as we found in the No-TMS experiment.

When TMS was delivered at the r-FEF site (Fig. 4*C*) simultaneously with the cue onset (TMS timing = 0 ms), participants continued to automatically adjust the focus of attention. The AG was still different between the 2 cue conditions (for the large cue: mean AG = −5.13 ms, SE = 6; for the small cue: mean AG = 26.13 ms, SE = 7; $F_{1,8} = 8.08$, $P < 0.05$, $\eta_p^2 = 0.50$). In contrast, when TMS was delivered to the r-FEF 70 ms after the cue onset, the AG did not differ between the large and the small cue condition (mean AG = 12.97 ms in the large cue, SE = 5; mean AG = 13.81 ms in the small cue, SE = 6; $F_{1,8} < 1$, n.s., $\eta_p^2 = 0.001$). Furthermore, in the r-FEF TMS condition, the AG differed significantly between the 2 TMS timing, for both the large ($F_{1,8} = 12.60$, $P < 0.05$, $\eta_p^2 = 0.61$) and the small cue condition ($F_{1,8} = 7.84$, $P < 0.05$, $\eta_p^2 = 0.49$). These results suggest that benefits associated with automatic control of the size of the attentional focus were selectively disrupted by TMS delivered 70 ms after the cue onset on the right FEF.

The ANOVA revealed also a main effect of Cue ($F_{1,8} = 10.29$, $P < 0.05$, $\eta_p^2 = 0.56$). No other main effect or interaction was significant.

Discussion

The focus of attention can be adjusted in its size to process information from a narrow (zoom-in) or a broad (zoom-out) region of the visual field. Two processes control the attentional zooming: an early, short-lasting process that automatically adjusts the focus of attention to the object size and a later, long-lasting process that voluntarily maintains attention on a focus (Turatto et al. 2000). However, the brain areas devoted to control the size of the attentional focus in striate and extrastriate visual cortex (Müller et al. 2003) have not been clarified yet. Our findings are the first prove that FEF plays a causal role in the automatic modulation of the attentional focus size.

Our behavioral results showed that when participants were induced to broaden their focus of attention onto a large cue, the "attentional gradient" (i.e., difference in RTs between the farthest and the nearest eccentricity) was nullified, indicating an efficient spread of attentional resources. On the other hand, when participants were induced to narrow their focus of attention onto a small cue, the attentional gradient arose, indicating an efficient zoom-in mechanism.

It is important to note that we observed a focus size-dependent modulation only at 100-ms cue-target SOA, while with longer SOAs the attentional zooming mechanism decayed, supporting the existence of a short-lasting process that automatically adjusts the focus of attention (Turatto et al. 2000). The same time course is present also in typically developing children (Ronconi, Gori, Ruffino, Molteni et al. 2012; Ronconi, Gori, Ruffino, Franceschini et al. 2012). These results show that the modulation of the attentional focus size was measured, rather than a simple perceptual facilitation due to the lateral small or large cue boundary. No theoretical reasons suggest that this perceptual facilitation should be present only at the first SOA. One could argue that the cue did not operate to focused or spread attentional resources, but simply served as an exogenous lateralized cue. This alternative hypothesis seems unfounded given the pattern of results. A lateralized facilitation in the large cue condition should induce an inverse attentional gradient (e.g., slower RTs near the fixation and faster RTs at the locus of the cue boards), whereas we found a flattened detection speed across eccentricities when participants spread their focus of attention.

In Experiment 2, we applied single-pulse TMS to interfere with the control of the attentional focus size. Our results clearly show that only TMS to the right FEF interferes with the modulation of the attentional focus size at the first cue-target SOA. When single-pulse TMS was delivered on right FEF 70 ms after the large cue onset, the attentional gradient persisted, demonstrating that the zoom-out of the attentional focus was impaired. Similarly, when single-pulse TMS was delivered on right FEF 70 ms after the small cue onset, the zoom-in mechanism was inhibited. On the contrary, when TMS was delivered simultaneously to the cue onset participants succeed in the automatic modulation of the size of their attentional focus according to the area delimited by the spatial cue.

The use of 2 different TMS timings was important because it allowed us to exclude indirect and nonspecific effects of FEF stimulation in early visual areas (Ruff et al. 2006, 2009). Only single-pulse TMS delivered 70 ms after the cue onset inhibited the regulation of the attentional focus size. The efficacy of the 70-ms TMS timing in interfering with the focus size modulation is compatible with the latencies of FEF neuron response after the onset of a visual stimulus (Bullier 2001). In contrast, the stimulation of the left FEF did not interfere with the modulation of the attentional focus size. The fact that TMS affects the attentional focus only when delivered on the right FEF, appears to be another strong argument against the interpretation of our results in terms of perceptual facilitation.

As attentional zooming modulates visual search (e.g., Greenwood and Parasuraman 1999), right hemisphere specialization in controlling the size of the attentional focus is consistent with previous studies revealing the causal role of the right FEF in visual conjunction search performance (e.g., Ashbridge et al. 1997; Muggleton et al. 2003). The present results are also in agreement with the evidence revealing the causal role of the right FEF in modulating the activity of the striate and extrastriate visual cortices (Ruff et al. 2006; Taylor et al. 2007).

Although our results demonstrated the role of the right FEF area in controlling the adjustment of the focus size, other areas could also be involved. Another possible candidate in playing a role in the attentional focus modulation could be the right posterior parietal cortex (PPC; e.g., Halligan and Marshall 1993; Taylor et al. 2007; Ruff et al. 2009). This area is an important component of the attentional network in human and nonhuman primates (e.g., see Vidyasagar 1999 for reviews; Bisley and Goldberg 2003; Saalmann et al. 2007), and it is strongly interconnected with the FEF (e.g., Buschman and Miller 2007; Kveraga, et al. 2007; see Corbetta and Shulman 2002, 2011 for reviews). Future researches could directly investigate the role of the PPC in the attentional focus control, employing a similar paradigm, but varying the TMS timing. In support of the role of PPC in the modulation of the attentional focus, Chen et al. (2009) employed a different experimental paradigm with fMRI and revealed shared activations for both zoom-in and zoom-out conditions in the right posterior temporoparietal junction. The combination of our findings and

the previous literature suggest that a right network of brain areas, including the FEF and PPC, could be involved not only in attentional orienting (Corbetta and Shulman 2002, 2011) but also in the attentional focus size control.

These findings have important implications for several neurodevelopmental disorders associated with attentional zooming dysfunctions. For example, autism spectrum disorders (ASD) have been repeatedly associated with different types of dysfunctions in spatial attention (see Ames and Fletcher-Watson 2010 for a review). In particular, previous studies found an impaired zoom-out attentional mechanism in children with ASD (Mann and Walker 2003; Ronconi, Gori, Ruffino, Molteni et al. 2012; Ronconi, Gori, Ruffino, Franceschini et al. 2012). One of the leading hypotheses about the neural disorders in ASD proposes that autistic brain is characterized by a short-range hyperconnectivity (i.e., within local neural districts) and long-range hypoconnectivity (i.e., across different brain areas; Belmonte et al. 2004). In particular, one of the most impaired long-range connections is between frontal and occipital lobes (e.g., Courchesne and Pierce 2005; Barttfeld et al. 2010). The present study, showing the critical role of right FEF in the attentional focus size control, supports the dysfunctional fronto-occipital connection hypothesis for the attentional zoom-out deficit in children with ASD.

Several evidence suggest a causal role of visual spatial attention also in developmental dyslexia (see Vidyasagar 1999; Facoetti et al. 2010; Vidyasagar and Pammer 2010 for reviews; Franceschini et al. 2012). Children with dyslexia exhibited a sluggish attentional zoom-in (e.g., Facoetti et al. 2000; Facoetti and Molteni 2001), as well as worse serial visual search performance (e.g., Vidyasagar and Pammer 1999). Recently, Zorzi et al. (2012) showed how enlarging the space between words and letters improve the reading abilities of the dyslexics. This simple text manipulation probably allows dyslexic readers to overcome the deficit in narrowing their attentional focus (Vidyasagar and Pammer 1999; Facoetti et al. 2000; Facoetti and Molteni 2001).

Thus, our TMS findings, demonstrating the critical role of the right FEF in the attentional focus size control, suggest that both ASD and dyslexia might be linked to a right frontoparietal dysfunction.

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Notes

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