

UNIVERSITA' DEGLI STUDI DI VERONA

DEPARTMENT OF

Neuroscience, Biomedicine and Movement Sciences

GRADUATE SCHOOL OF

Life and Health Sciences

DOCTORAL PROGRAM IN

Neuroscience, Psychological and Psychiatric Sciences, and Movement Sciences

XXXV cycle/year 2019

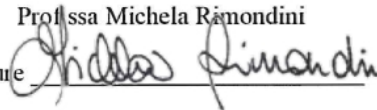
TITLE OF THE DOCTORAL THESIS

“TEMPORAL DYNAMICS OF TARGET SELECTION AND DISTRACTOR
SUPPRESSION MECHANISMS IN THE RIGHT FRONTAL EYE FIELD”

S.S.D. BIO/09

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Sommario

La capacità del cervello umano di selezionare attivamente le informazioni rilevanti ignorando gli elementi distraenti ed irrilevanti è essenziale per portare a termine con successo le attività quotidiane. Il presente progetto di dottorato ha come scopo quello di svelare le dinamiche temporali della selezione del target e della soppressione del distrattore nel Frontal Eye Field (FEF), un'area cruciale del circuito attenzionale frontoparietale. Uno studio precedente (Lega et al., 2019) ha indagato il contributo di IPS (Intraparietal Sulcus) e FEF nei meccanismi di attenzione visuo-spaziale tramite l'applicazione di treni da 3 impulsi di TMS a 10 Hz durante un compito di ricerca visiva. La stimolazione è stata somministrata in una finestra temporale che andava dai 100 ai 300 ms dopo la comparsa degli stimoli, in quanto tale epoca post-stimolo è considerata cruciale per i processi attentivi implicati nella ricerca visiva. Tale studio ha rivelato che la TMS è stata efficace nel migliorare i meccanismi di soppressione del distrattore, riducendo il costo causato dall'esperire uno stimolo saliente ma irrilevante rispetto agli scopi del compito.

Per chiarire ulteriormente il contributo temporale del FEF destro alla soppressione della distrazione, sono stati condotti due esperimenti. L'Esperimento 1 ha applicato singoli impulsi TMS sul FEF destro in tre diversi istanti temporali, precisamente 50, 200 o 350 ms dopo la comparsa del *search array*. L'Esperimento 2 era mirato ad esercitare un effetto della TMS più forte sul FEF destro, mantenendo comunque la medesima puntuale indagine temporale. Pertanto, nell'Esperimento 2 sono stati applicati treni da tre impulsi di TMS a 20 Hz sul FEF destro in tre diverse finestre temporali: da -50 a 50 ms (T1), da 100 a 200 ms (T2), da 250 a 350 ms (T3) dopo la comparsa del *search array*.

Mentre l'Esperimento 1 ha mostrato solo un effetto generale, temporalmente aspecifico e quasi significativo della stimolazione sui tempi di reazione, l'Esperimento 2 ha rivelato che la stimolazione a T2 (100-200 ms) era associata a

un aumento del costo della distrazione, in particolare per gli stimoli distrattori localizzati contralateralmente al sito di stimolazione.

Questi risultati supportano il ruolo del FEF destro nel sopprimere la distrazione scaturita da stimoli salienti ma irrilevanti e suggeriscono che l'applicazione della TMS sia in grado di inibire quella rete neurale che regola e limita l'interferenza generata da tali elementi distraenti. Ulteriori ricerche sono necessarie per valutare con precisione gli effetti fisiologici di diversi protocolli TMS sul FEF destro e le sue influenze sulle computazioni di carattere attentivo.

Abstract

The ability of the human brain to selectively attend to relevant information while ignoring irrelevant distraction is essential for the successful completion of everyday tasks. The present PhD project aimed to unravel the temporal dynamics of target selection and distractor suppression in the Frontal Eye Field (FEF), a key node in the dorsolateral attention network. Previous research (Lega et al., 2019) had assessed the contribution of both IPS and FEF to the deployment of visuo-spatial attention by means of 10 Hz TMS during a visual search task. The stimulation was delivered in a post-stimulus epoch from 100 to 300 ms, considered crucial for attentional computations in visual search. This study found that the TMS protocol improved distractor suppression mechanisms, reducing the cost engendered by salient but task-irrelevant distractors.

To further clarify the temporal contribution of right FEF to distractor suppression, two experiments were carried out. Experiment 1 applied single-pulse TMS over right FEF at three different time points, 50, 200 or 350 ms after search array onset. Experiment 2 aimed to exert a stronger TMS effect over right FEF while maintaining a temporal-punctate approach. It applied trains of triple-pulse TMS at 20 Hz over right FEF in three different time windows: from -50 to 50 ms (T1), from 100 to 200 ms (T2) and from 250 to 350 ms (T3) after the search array onset.

While Experiment 1 showed only a general, time-unspecific and quasi-significant effect of stimulation over response times, Experiment 2 revealed that stimulation at T2 (100-200 ms) was associated with an increase of the distractor cost, specifically for distractors located contralaterally to the stimulation site.

These findings support the role of right FEF in suppressing distractions from salient but irrelevant stimuli and suggest that TMS may activate/inhibit the neural network that regulates and limits interference from such distractions. Further research is needed to precisely assess the physiological effects of different TMS protocols of the right FEF and its influence on attentional computation.

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Preface

How does the brain manage to filter out distractions and keep us focused on the task at hand? This question has intrigued me since the beginning of my academic journey, and has been the driving force behind my research in cognitive neuroscience. I embarked on this quest during my master's degree at the University of Padova, where I had the opportunity to investigate the ocular correlates of Mind Wandering, an internal source of distraction that can impair task performance.

My passion for understanding how the brain copes with distractions grew further during my doctoral studies in Neuroscience, Psychological and Psychiatric Sciences, and Movement Sciences at the University of Verona, under the guidance of Prof. Leonardo Chelazzi. Here, I was able to expand my knowledge and investigate how people counteract external distraction, with a particular focus on attentional control and its underlying neural mechanisms.

However, my path was not without its challenges. The outbreak of the pandemic at the very beginning of my PhD program heavily impacted on the ability to run experiments on human subjects, which is a crucial aspect of my research. As a result, the number of experiments I was able to carry out is limited. Nevertheless, I persevered and worked tirelessly to complete this thesis, knowing that the findings presented here could make a valuable contribution to the field of visual spatial selective attention.

This thesis represents the culmination of my efforts and my passion for understanding the workings of the human brain. It is my hope that it inspires others to continue exploring the mysteries of the mind and to persevere through challenges to achieve their academic goals.

Part 1

Theoretical background

1. Visual selective attention

Our daily lives involve a constant barrage of visual input, and attention helps us to make sense of this vast amount of information. Each piece of information competes for our attention, but only a small portion is ultimately able to reach our awareness. Given that our cognitive resources are limited, our nervous system employs a "gating" mechanism to prioritize the processing of relevant information over less important stimuli. This helps us focus on specific parts of the visual field and select (and process) the most relevant information while ignoring irrelevant but attention-grabbing stimuli (Jonides & Yantis, 1988; Yantis & Jonides, 1990; Forster & Lavie, 2008; Marini, Chelazzi & Maravita, 2013; Carrasco, 2011).

For example, if you are walking down a busy city street, your attention may be focused on the task of navigating through the crowds of people and avoiding collisions. You might be able to tune out the sights and sounds of other distractions, such as advertising billboards or people selling products on the street. This is because your nervous system is designed to prioritize the processing of information that may be relevant to your survival or well-being. In this way, attention helps us orient ourselves in the "jungle" of information that surrounds us and make sense of the world around us. However, if something unexpected or unusual catches our eye, such as a person falling or a car speeding toward you, our attention will likely be automatically drawn to this salient stimulus.

2. Bottom-up and top-down control of attention

Traditionally, attention has been thought to be controlled either through a bottom-up or a top-down mechanism. Bottom-up attention refers to the automatic and involuntary process of directing attention toward stimuli based on their physical characteristics, including their location, size, color, orientation or brightness (*stimulus-driven attention*; Yantis & Yonides, 1984; Theeuwes, 2010; Franconeri & Simons, 2003). This type of attention is thought to be driven by the

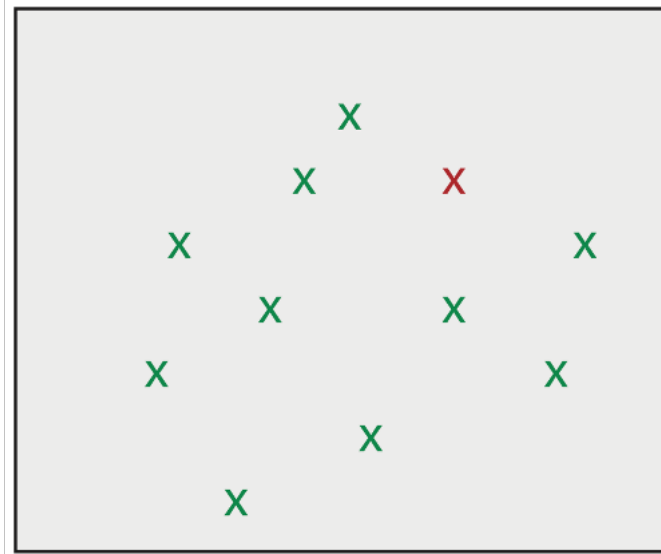


Figure 1. Representation of a feature-based visual search task. Adapted from Eckstein (2011).

salience of a stimulus, meaning that it stands out in some way compared to its surroundings. An example of bottom-up attention can be seen in the "pop-out" effect, where an individual is able to quickly locate and identify a target stimulus that is different e.g. in color or shape compared to the surrounding stimuli (Theeuwes, 2010). On the other hand, top-down attention refers to the voluntary and goal-directed process of directing attention toward specific stimuli or tasks. This type of attention is guided by an individual's current goals, expectations, and intentions, and can be influenced by prior knowledge and experience (*goal-driven attention*). For example, if an individual is searching for a specific object in a cluttered environment, they will use top-down attention to focus on specific features or locations that are relevant to their search goal (Egeth & Yantis, 1997). Top-down attention can also be influenced by context, as in the case of "contextual cueing", where an individual is faster at locating a target in a familiar versus unfamiliar environment (Folk et al., 1992).

As I previously said, *stimulus-driven attention* is attracted to stimuli that stand out from the background due to their distinctive physical appearance (Treisman,

1988; Wolfe, 1994). An example of this attentional control mechanism can be seen in a visual search task, where the goal is to quickly and accurately locate the target item among a group of distractors. When the target is a singleton stimulus, attention is solely guided by the salience of its physical properties, without any voluntary effort on the part of the observer. The surrounding elements, or distractors, are simply filtered out because they lack the defining feature of the target. An example of this can be seen in Figure 1, where the task of identifying the red "x" target is made easy because the target's physical property makes it stand out among the other stimuli. In this case, the feature integration theory suggests that simple stimulus features such as color, luminance, and orientation are processed in different areas within the visual cortex, allowing for the simultaneous processing of the "pop-out" stimuli without the need for serial examination of each element in the display (Duncan & Humphreys, 1989; Treisman & Gelade, 1980).

On the other hand, when the target is not defined by a salient property, we need to guide attention toward the task-relevant item through a top-down (goal-driven) mechanism. Top-down attentional control is driven by the voluntary selection of elements that are relevant to the individual's goals (e.g., Folk et al., 1992; Bacon & Egeth, 1994; Egeth & Yantis, 1997; Folk & Remington, 1998; Corbetta & Shulman, 2002; Reynolds & Heeger, 2009; Carrasco, 2011). The endogenous cueing paradigm, first introduced by Posner (1980), provides early evidence for this type of attentional control (as shown in Figure 2). In this task, a centrally-placed visual cue (such as an arrow) signals the likely location of an upcoming target. Faster and more accurate responses are observed when the target appears in the cued location (valid condition) compared to when it appears in the uncued location (invalid condition). This suggests that the valid condition leads to facilitated processing of the target located where attention has been previously allocated, while the invalid condition requires a shift of attention from the cued location to the location of the actual target.

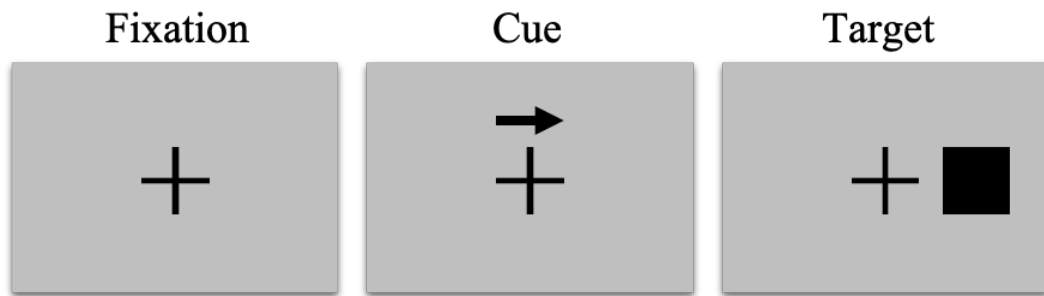


Figure 2. Schematic representation of Posner (1980) endogenous cueing task.

While the traditional division between top-down and bottom-up attentional control has long been established, recent insights have highlighted the inadequacy of this dichotomy in comprehensively explaining the complexities of attention allocation. In fact, attention can be significantly influenced by past interactions with the environment, which, in turn, play a role in guiding current and future target selection (Awh et al., 2012; Ferrante et al., 2018; Jiang, 2018). Recent studies have demonstrated that there are multiple factors that influence the allocation of attention. These factors include stimulus-driven signals such as salience (Chelazzi et al., 2011; Reynolds & Heeger, 2009), goal-driven signals like task instructions (Reynolds & Heeger, 2009; Desimone & Duncan, 1995), selection history (Maljkovic & Nakayama, 1994; Theeuwes & Van Der Burg, 2011; Hillstrom, 2000), reward and motivation (Pessoa & Engelman, 2010; Anderson et al., 2011; Chelazzi et al., 2013; Chelazzi et al., 2014; Bourgeois et al., 2016), emotional value (Pessoa et al., 2002a; Pessoa et al., 2002b; Mancini et al., 2020, 2022; Mirabella, 2018; Mirabella et al., 2022; Calbi et al., 2022), and statistical learning (Fiser & Aslin, 2001; Saffran, 1996; Jiang, 2018; Ferrante et al., 2018; Geng & Behrmann, 2005; Dolci et al., 2021). As a result, a third mechanism of attentional control has been proposed: experience-dependent attentional control (Awh et al., 2012; Failing & Theeuwes, 2018; Chelazzi & Santandrea, 2018; Dolci et al., 2021). This mechanism takes into account the various factors that might contribute to the deployment of attention, above and beyond bottom-up and top-down control.

For example, in a study by Pessoa and Engelman (2010), participants were more likely to attend to stimuli that were associated with a reward, even when the stimuli were not particularly salient. This evidence suggests that motivation can exert a certain influence over attentional control. Likewise, the emotional significance of stimuli can influence attention allocation. Multiple studies have illustrated that both emotional facial expressions (Mancini et al., 2020, 2022; Mirabella, 2018; Mirabella et al., 2022) and body postures (Calbi et al., 2022, Mirabella et al., 2022) can impact behavior, but only when they are relevant to the ongoing task. For instance, in a study by Mirabella (2018) and Mancini et al. (2020), they employed a Go/No-go task to reveal that fearful facial expressions led to increased reaction times and a higher number of omissions compared to positive facial expressions. However, when participants were instructed to discern the gender of the displayed face, irrespective of its emotional expression, no differences were observed between positive and fearful facial expressions. This highlights the notion that the response to emotional stimuli is intricately linked to a conscious evaluation.

As already mentioned, also learning statistical regularities in the environment could exert an influence over the behavior. Statistical learning (SL) enables individuals to implicitly identify regularities in sequences of elements or movements within their environment (Fiser & Aslin, 2001; Saffran, 1996; Jiang, 2018; Ferrante et al., 2018; Geng & Behrmann, 2005). This phenomenon was firstly observed in the acoustic domain, particularly in language and vocabulary acquisition, where individuals, even infants, exhibit the ability to implicitly learn structural patterns in speech and visual scenes (Saffran et al., 1999; Saffran, 2001; Horn et al., 2004; Aslin & Newport, 2012).

In the domain of visual attention, SL is closely linked to the frequency of appearance of specific elements at particular spatial locations. This form of SL enhances efficiency in identifying visual targets when they appear at frequently occurring locations (Ferrante et al., 2018; Geng & Behrmann, 2005; Jiang, 2018;

Di Caro et al., 2019). In Geng and Behrmann (2005) the researchers manipulated the location of a target "T" among "L" signs. The target appeared in a high-probability location 75% of the times and in low-probability locations 25% of the times. The results showed that participants were faster and more accurate at detecting the target when it appeared in the high-probability location. Again, these results were confirmed by Ferrante and colleagues (2018) who found that this effect can occur rapidly, even after a limited number of trials. Additionally, studies showed that the effects of SL on target location persist even after the frequency of the target is no longer unequal (Jiang et al., 2013; Jiang et al., 2014; Ferrante et al., 2018). Furthermore, SL not only influences target selection but also shapes the filtering of distractors. Studies have shown that individuals assign different attentional priorities to spatial locations based on SL, including "de-prioritizing" locations with frequent interference (Reder et al., 2003). Consequently, salient distractors appearing in high-frequency locations are actively suppressed, reducing interference (Reder et al., 2003).

Overall, it is clear that attentional control is not solely determined by bottom-up or top-down mechanisms, but rather by a complex interplay of multiple factors. Understanding the influence of these factors is important for understanding how attention is deployed in various contexts.

3. Attentional capture

A growing body of literature is aimed to assess the interaction between the above-mentioned attentional control signals in the deployment of attention. Particularly, efforts are put into discerning whether such signals are independent forms of attentional control, or whether they may cooperate in the attentional computations (Corbetta & Shulman, 2002; Theeuwes & Belopolsky, 2010; Theeuwes & Godijn, 2001; Raushenberger, 2003; Burnham, 2007). Indeed, there are certain scenarios where the bottom-up control exerts its influence regardless of the top-down attentional set actively engaged. A task that sheds light on such

phenomenon is the so-called *additional singleton paradigm* (Theeuwes, 2010). The task (Figure 3) is characterized by two singleton stimuli presented in an array of homogenous distractor items, with the two singletons differing from the distractors in color and shape, respectively. Subjects were instructed to discriminate the orientation of the black bar within the target stimulus, which might be one of the singleton items depending on task instructions. Interestingly, this task provided evidence that faster and more accurate responses were

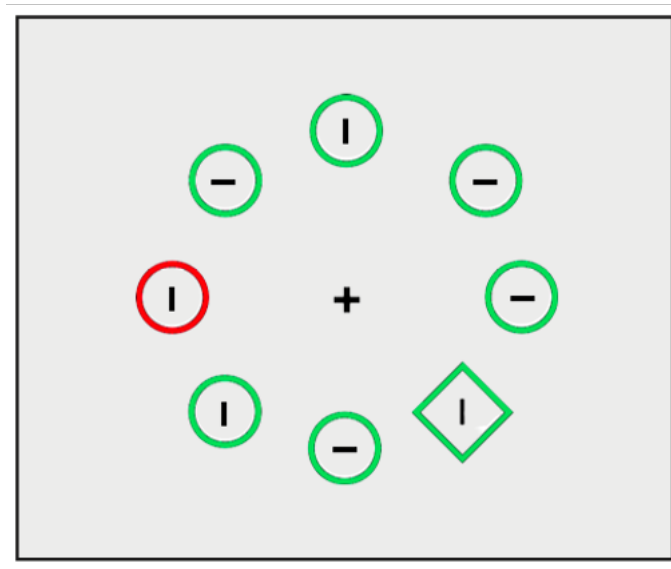


Figure 3. Additional singleton paradigm. Adapted from Theeuwes (2010)

associated with the color-singleton target relative to the shape-singleton one, indicating that in the latter context, the selection of the salient but irrelevant color singleton happened regardless of whether the top-down attentional set was engaged. This kind of unintentional selection of a salient yet task-irrelevant stimulus is the so-called *attentional capture* effect (Theeuwes, 1992).

In the example shown in Figure 4, the target is the only circle-shaped item embedded in an array of diamond-shaped distractors. A possible way to

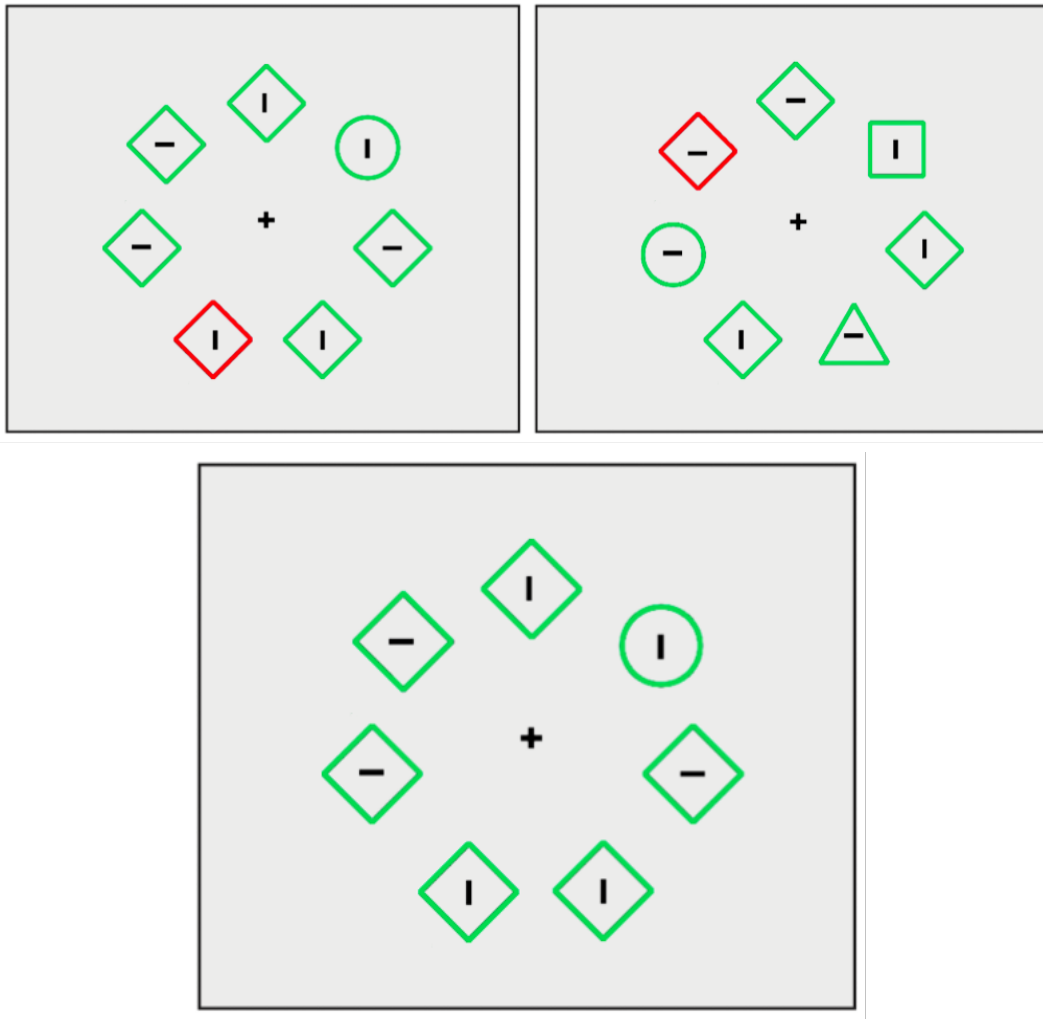


Figure 4. Singleton-detection strategy. Adapted from Bacon & Egeth (1994).

individuate the target may be looking for the odd stimulus (circle among diamonds) instead of looking for the stimulus with certain features (the item being circle-shaped). Such strategy is the *singleton-detection mode*, which led the observer to look for any color or shape singleton in the scene. However, in the case of multiple singleton stimuli displayed, this kind of strategy may lead to unintentional attentional capture by salient but task-irrelevant stimuli. In this respect, the study of Bacon and Egeth (1994) showed less interference engendered by the salient distractor if an attentional set tuned to a specific feature of the target (*feature-detection mode*) is engaged. In the example shown in Figure 5, the target

was always the circle-shaped item among several different-shaped stimuli, making a feature-based target search more effective than a singleton search strategy - avoiding eventual attentional capture by any singleton stimuli that are not the desired target.

4. Distractor suppression

In the previous chapter, it was mentioned that the attentional capture theory posits that unintentional shifts of attention toward salient distractors occur regardless of the observer's will (Theeuwes, 1992). However, engaging in a *feature-detection mode* while searching for the target results in less interference from a salient, but irrelevant, stimulus (Bacon & Egeth, 1994). This suggests that in some cases, it is possible to suppress the influence of distractors, which contradicts the idea of attentional capture proposed by Theeuwes in 1992.

To reconcile these conflicting viewpoints, Luck and colleagues (Sawaki & Luck, 2010; Gaspelin & Luck, 2018a; Gaspelin & Luck, 2018b) proposed a model in which any salient stimuli can automatically trigger an "attend-to-me" signal, which can be suppressed through the use of top-down attentional control to avoid attentional capture. This model represents a compromise between stimulus-driven and goal-driven theories of attentional capture, as it acknowledges the ability of salient stimuli to automatically capture attention, while also recognizing the role of top-down control in suppressing such capture.

Distractor suppression is the ability to ignore or disregard salient distractions while focusing on task-relevant information (Chelazzi, Marini, Pascucci & Turatto, 2019). It is an important aspect of selective attention that involves the reduction or elimination of the negative impact of irrelevant but salient stimuli on behavior (Lega et al., 2019; Chelazzi et al., 2019). In recent years, numerous mechanisms for distractor suppression have been proposed, including intertrial priming (Geyer, Müller & Krummenacher, 2008; Müller et al., 2010), proactive

and reactive control (Marini et al., 2013; Marini, Demeter, Roberts, Chelazzi & Woldorff, 2016; Geng, 2014; Cosman, Lowe, Zinke, Woodman & Schall, 2018), habituation of capture (Neo and Chua, 2006; Pascucci & Turatto, 2015; Turatto, Bonetti, Pascucci & Chelazzi, 2018), and implicit distractor probability learning (Goschy, Bakos, Muller & Zehetleitner, 2014; Ferrante et al., 2018; Wang & Theeuwes, 2018; Sauter et al., 2018, 2019; Di Caro et al., 2019).

For example, intertrial priming involves the influence of previous experiences with stimuli on current behavior (Geyer, Müller & Krummenacher, 2008). When an individual has previously (e.g., on the previous trial) encountered a stimulus and successfully ignored it, they are more likely to do so again in the future, resulting in improved distractor suppression. Proactive control, on the other hand, involves the proactive maintenance of task-relevant information in working memory to facilitate the suppression of distractions (Marini et al., 2013; Marini, Demeter, Roberts, Chelazzi & Woldorff, 2016; Geng, 2014; Cosman, Lowe, Zinke, Woodman & Schall, 2018). For instance, if an individual is engaged in a task that requires them to remember certain details, they may be more able to disregard distractions due to their proactive control of task-relevant information.

Habituation of capture is a mechanism of distractor suppression that occurs as a result of repeated exposure to a stimulus. Essentially, this means that as an individual is presented with the same salient distractor over and over again, their attention becomes less likely to be captured by it. This process is known as habituation, and it is thought to be a result of the brain's ability to adapt to repeated stimuli by decreasing the response to them (Neo and Chua, 2006; Pascucci & Turatto, 2015; Turatto, Bonetti, Pascucci & Chelazzi, 2018). Implicit distractor probability learning refers to the influence of the likelihood of encountering a distractor on the ability to suppress it (Goschy, Bakos, Muller & Zehetleitner, 2014; Ferrante et al., 2018; Wang & Theeuwes, 2018; Sauter et al., 2018, 2019; Di Caro et al., 2019). If an individual expects to encounter a certain type of distractor with various probabilities across the different locations in the

visual display, they may be more able to ignore it when it does appear at a high probability location, due to their learned probability of encountering it.

5. The neural basis of distractor suppression

The neural basis of distractor suppression has been extensively studied in recent years. There is a growing body of literature that suggests that the dorsal frontoparietal attention network, which includes the frontal eye field (FEF) and the posterior parietal cortex (PPC), plays a key role in modulating attentional capture elicited by salient distractor stimuli Corbetta & Shulman, 2002; de Fockert, Rees, Frith & Lavie, 2004; Serences, Yantis, Culbertson & Awh, 2004; Serences et al., 2005; Leber, 2010; Talsma, Coe, Munoz & Theeuwes, 2010; de Fockert & Theeuwes, 2012; DiQuattro, Sawaki & Geng, 2014; Marini et al., 2016; Lee and Geng, 2017).

Brain imaging studies have suggested that there is a link between frontal regions and neural activity related to distractor suppression. In tasks that require focusing on a specific target, activity in the prefrontal cortex (PFC) tends to be higher when there are irrelevant distractions present, as pointed out by De Fockert and colleagues (2004). Furthermore, the magnitude of brain activity in the PFC seemed to be linked to the degree of interference engendered by salient distractors (Leber, 2010; de Fockert and Theeuwes, 2012). The study of Marini and colleagues (2016) found that activity in the right PFC, specifically the rIFG and rMFG, predicted the magnitude of interference caused by salient distractors in a visual search task. These findings are consistent with neuropsychological evidence indicating that the rMFG plays a crucial role in regulating both top-down and bottom-up attention (Japee et al., 2015).

Several brain stimulation studies have been conducted to establish a causal relationship between the dorsal frontoparietal attention network and distractor suppression. For example, in the study of Cosman, Atreya & Woodman (2015),

the researchers applied anodal transcranial direct-current stimulation (tDCS) to the bilateral prefrontal cortex (PFC), a key region of the dorsal frontoparietal attention network. They found that tDCS to the PFC was associated with a reduction in the behavioral cost caused by the presence of salient but task-irrelevant stimuli. Another study, by Hodsoll, Mevorach & Humphreys (2009), used repetitive transcranial magnetic stimulation (rTMS) applied to the posterior parietal cortex (PPC), another key region of the dorsal frontoparietal attention network. They found that rTMS applied to the right PPC (but not the left PPC) resulted in a reduction in the behavioral cost of distraction. These studies suggest that the dorsal frontoparietal attention network plays a significant role in distractor suppression, and that brain stimulation techniques are effective at interfering with the attentional processes housed by these areas.

Several studies using electroencephalography (EEG) have found evidence of two event-related potential (ERP) components, the N2pc and the Pd (distractor positivity), that are associated with the suppression of salient distractors (Figure 6). The N2pc component is a transient negative increase in activity over posterior electrode sites (typically PO7/8) that is contralateral to the attended object and peaks around 200 milliseconds after the onset of the stimulus (e.g., Luck and Hillyard, 1994; Eimer, 1996; Woodman and Luck, 1999, 2003; Töllner et al., 2012; Liesefeld et al., 2017). The Pd (distractor positivity) component is a positive increase in activity contralateral to the distractor over the same posterior electrode sites, which is thought to reflect an active suppression mechanism that is used to disengage attention from the salient distractor (Gaspar and McDonald, 2014; Hickey et al., 2009; Jannati et al., 2013; Sawaki et al., 2012; Toffanin et al., 2011; Liesefeld et al., 2017).

In the study by Liesefeld and colleagues (2017), the temporal dynamics of the N2pc and Pd ERP components were investigated in a visual search task in which participants had to discriminate a salient target in the presence of a salient but irrelevant distractor. The results of the study showed that there is a clear sequence

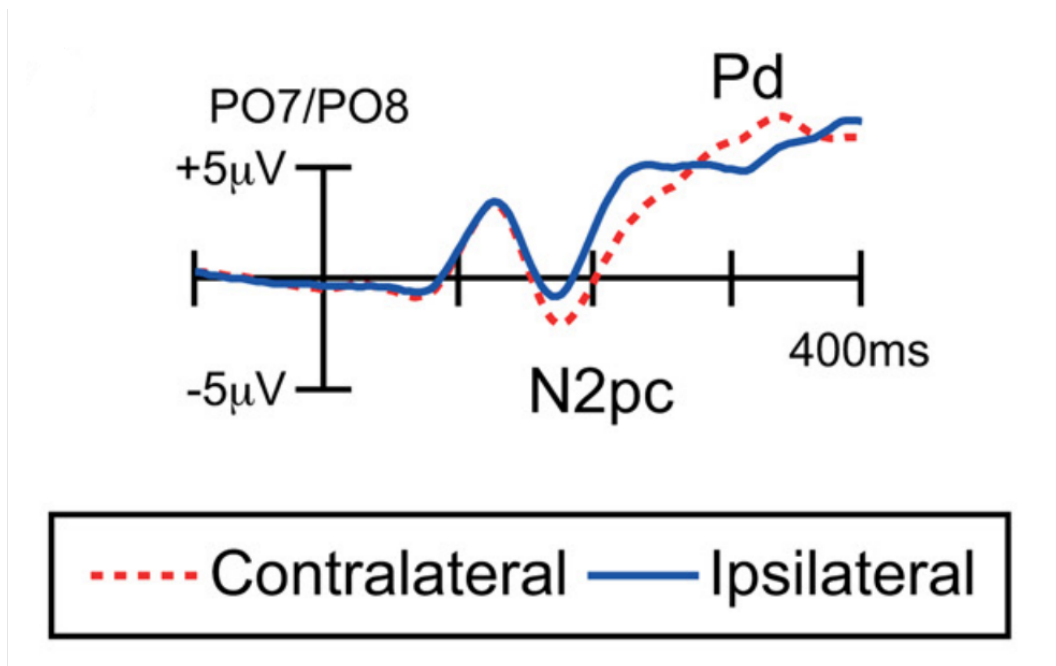


Figure 6. ERP component of target selection (N2pc) and distractor suppression (Pd). Adapted from Sawaki et al., (2012).

of attentional mechanisms involved in the process of dampening attentional capture and shifting attention back to the target. Specifically, the pattern was characterized by:

1. The appearance of a distractor N2pc, which signals that attention has been captured by the salient distractor.
2. The emergence of the Pd component immediately after the distractor N2pc, which indicates an active top-down suppression mechanism being used to disengage attention from the salient distractor. This component is a positive increase in activity contralateral to the distractor over the same posterior electrode sites, which is thought to reflect an active suppression mechanism.

3. The appearance of a final target N2pc after the two aforementioned components which indicates that the target has been reliably attended to, even if attention was initially drawn away by the distractor.

Overall, these findings suggest that in the presence of a salient but irrelevant distractor, attention is automatically captured by the stimulus (as indicated by the distractor N2pc), but the distractor's representation is then efficiently suppressed (as indicated by the Pd component) in order for attention to be shifted back to the target (as indicated by the target N2pc).

6. The role of the Frontal Eye Field in the selection of the target and in suppressing irrelevant distractors

The Frontal Eye Field (FEF) is a brain area located in the dorsal portion of the prefrontal cortex, which plays a crucial role in the control of eye movements and visual attention. Over the past few decades, researchers have used various techniques, including neurophysiological recordings in monkeys, functional magnetic resonance imaging (fMRI), and Transcranial Magnetic Stimulation (TMS) in humans, to study the FEF's contribution to target selection and distractor suppression.

One of the earliest studies to demonstrate the involvement of the FEF in target selection was conducted by Schall and colleagues in 1995. This study used single-unit recording in macaques to investigate the neural activity of the FEF during the performance of a visual search task. The study found that the initial visual response of FEF neurons was modulated by the presence of multiple stimuli and by whether a saccade was going to be produced, but the initial visual response did not discriminate the target of the search array from the distractors. In the latent period before saccade initiation, the activity of most visually responsive cells evolved to signal the location of the target. In Thompson, Bichot, and Sato (2005), they found that even when the monkey was instructed to maintain fixation and not

make a saccade, the FEF neurons were still able to selectively respond to the target stimulus. This suggests that the FEF plays a role in target selection independent of saccade production. In more recent years, neuroimaging techniques such as fMRI have been used to further investigate the involvement of the human FEF in target selection. For example, Kincade and colleagues (2005) did find evidence of activation in the Frontal Eye Field (FEF) in response to attentional shifts. The study used fMRI to investigate the neural mechanisms underlying attentional orienting, and found that different regions of the brain were activated depending on whether the attentional shift was voluntary or stimulus-driven. The FEF was found to be activated during both types of attentional shifts, but to a greater extent during voluntary shifts. This suggests that the FEF plays a role in the voluntary control of attentional shifts, although other regions such as the parietal cortex also appear to be involved. A great contribution to this topic comes from several non-invasive brain stimulation studies. Muggleton and colleagues (2003) sought to examine the involvement of the FEF in visual search tasks. They utilized repetitive Transcranial Magnetic Stimulation (rTMS) to disrupt normal FEF function while participants engaged in visual search tasks that did not necessitate saccades or eye movements. The study found that rTMS applied to the FEF impacted performance on a conjunction search task and a simple feature search task, where the target was not predictable from trial to trial, primarily by increasing false alarm rates. These findings confirm again that the human FEF plays a crucial role in visual selection, regardless of the need to generate a saccade command.

In addition to its role in target selection, subsequent studies have provided further evidence for the involvement of the FEF also in distractor suppression. A study by Hung, Driver, and Walsh (2011) used TMS to temporarily disrupt the activity of the FEF, bilaterally, in healthy participants while they performed a visual partial report task. The task required participants to selectively attend to and report a specific subset of visual stimuli presented within a larger display. The main findings of the study were that TMS to the right, and not left, FEF led to

increased distraction by irrelevant stimuli, resulting in a decline in performance on the visual partial report task. Specifically, the results showed that TMS applied to the right FEF led to a decrease in the ability to selectively attend to and report the target stimuli, as well as a reduction in the ability to suppress the influence of irrelevant distractors. Such evidence aligns well with the results provided by the study of DiQuattro et al., (2011; 2014), which reported an excitatory pathway from the temporoparietal junction to IFG and FEF being involved in the suppression of salient distractors. Interestingly, evidence from single-unit recordings in monkeys showed that FEF is involved both in target selection and distractor suppression during a visual search task (Cosman et al., 2018). This study found that when the salient distractor was successfully ignored, a robust suppression of its representation was observed in the FEF. This suppression occurred before it appeared in extrastriate visual areas, and was observed in neurons that also contributed to selecting the target, suggesting that a common mechanism in the FEF is responsible for both selecting task-relevant information and suppressing task-irrelevant information in sensory cortex.

7. The work of Lega et al., (2019)

An interesting study that sought to determine the contribution to target selection and distractor suppression of the two key nodes of the dorsal frontoparietal attention network - namely the FEF and IPS - was the work of Lega and colleagues (2019). Here four different brain sites - right and left FEF, right and left IPS, were targeted with TMS while participants performed a visual search task. The search display consisted of four stimuli (one per quadrant) presented equidistantly from each other. In half of the trials, all stimuli were of the same color (distractor-absent condition), whereas in the other half, there was one different-color stimulus among three same-color stimuli (distractor-present condition). Participants were asked to quickly and accurately identify the orientation of the target stimulus, which was defined by the pointing direction of the two triangles that composed it. The stimulation consisted of a 10 Hz triple-pulse TMS delivered in a precise time window that went from 100 to 300 ms after the search array onset, covering a post-stimulus period that is thought to be crucial for attentional computation (Jannati et al., 2013; McDonald et al., 2013; Liesefeld et al., 2017).

The study by Lega et al. (2019) provided intriguing results regarding the role of the right FEF in regulating attention during a visual search task. The results showed that stimulation of the right FEF led to a significant decrease in behavioral interference caused by task-irrelevant, salient distractors. This effect was not replicated when the left FEF was stimulated, as there was no discernible difference in attentional capture compared to the sham condition. Additionally, the results revealed that the extent of the decrease in distractor interference resulting from right FEF stimulation was correlated with the distance between the stimulation site and the primary motor cortex (M1) at the individual subject level, reaching a maximum at approximately 2.77 cm. The researchers also found that the reduction in distractor cost following right FEF stimulation was due to performance improvements exclusively in the distractor-present condition, which

demonstrates the specificity of such results. Furthermore, the results indicated that the greatest reduction in distractor interference was seen when the trial history was taken into account during stimulation of the right FEF.: when the previous trial was a distractor-absent trial, the distractor cost was effectively more reduced relative a situation where the preceding trial was characterized by the presence of a salient distractor. These findings support the idea that the right FEF plays a crucial role in limiting attentional capture by salient distractors and modulating distractor interference based on prior trial history. The study aligns with previous research that suggests that the prefrontal cortex plays a key role in controlling and filtering task-irrelevant information (Grosbras and Paus, 2003; Capotosto et al., 2009; Silvanto et al., 2006; Duecker et al., 2013; Wang et al., 2016; Marshall et al., 2015).

8. Aim of the project

The ability of the human brain to selectively attend to relevant information while ignoring irrelevant distractions is essential for the successful completion of everyday tasks. A wealth of research has highlighted the involvement of the frontal eye fields (FEF) in both the selection of targets (Schall et al., 1995; Thompson et al., 2005; Kincade et al., 2005; Muggleton et al., 2003) and the suppression of task-irrelevant distractors (Lega et al., 2019; Hung, Driver & Walsh, 2011; Cosman et al., 2018). The primary goal of my PhD project was to examine the temporal dynamics of these two mechanisms within the same neural network. Specifically, I aimed to investigate how the FEF is involved in the selection of targets and the suppression of distractors, and how these processes interact over time. I aimed to explore the neural mechanisms underlying these processes by means of time-punctate transcranial magnetic stimulation (TMS). Specifically, the first experiment applied single-pulse TMS at three different time points, while the second study employed a triple-pulse stimulation in three distinct time epochs. In light of our research objectives, we intentionally chose to prolong the stimulation time window in both Experiment 1 and Experiment 2, a departure from the approach adopted by Lega et al. (2019). Our rationale behind this methodological modification was driven by our intent to maximize our possibility to interact and distinguish among distinct attentional mechanisms, including attentional capture, target selection, and distractor suppression. In contrast to Lega and his colleagues (2019), who concentrated on a time window spanning from 100 to 300 ms after the stimulus, both Experiment 1 and Experiment 2 expanded the range to 50-350 ms.

Part 2

Experiments

1. Experiment 1

1. Methods

Participants Thirty healthy naïve participants (mean age = 24.03, SD = 4.09, 20 females) were tested. All participants were right-handed and with normal or corrected-to-normal vision. Before the TMS experiment, all participants filled out a safety screening questionnaire (Rossi, Hallett, Rossini & Pasqual-Leone, 2009), in order to exclude possible contraindications to the TMS application. The study was approved by the local Ethics Committee (Department of Neuroscience, Biomedicine and Movement Sciences, University of Verona) and conducted in accordance with the Declaration of Helsinki. Informed consent was obtained from all individual participants included in the study.

Materials and stimuli. The task was an adapted version of the *additional singleton paradigm* (Theeuwes, 1992). Here we used the same paradigm as in Lega et al., (2019). The visual search display was characterized by four stimuli (one per quadrant) presented equidistantly from each other and located at a distance of 4° from the center. In half of the trials, all stimuli were of the same color (distractor-absent condition), whereas in the other half, there were three same-colored stimuli and one different-colored stimulus (additional singleton distractor; distractor-present condition). All stimuli were composed of two triangles: the target was the only item with both triangles pointing in the same direction, while the distractor – when present – was characterized by pointing outwardly triangles. The remaining stimuli (non-target stimuli or fillers) were composed of pointing inwardly triangles (Figure 7).

Procedure Participants were seated on a chair facing a 17-inch CRT monitor (1280 x 1024 pixels, 75 Hz) at a distance of 60 cm. Head movements were prevented by a chinrest during the whole experiment. Each trial started with the presentation of a central fixation point for 1000 ms, followed by a display of four placeholders (identical to the non-target stimuli) that lasted 700 ms. Next, the target took the place of one of the four placeholders; in the distractor-present

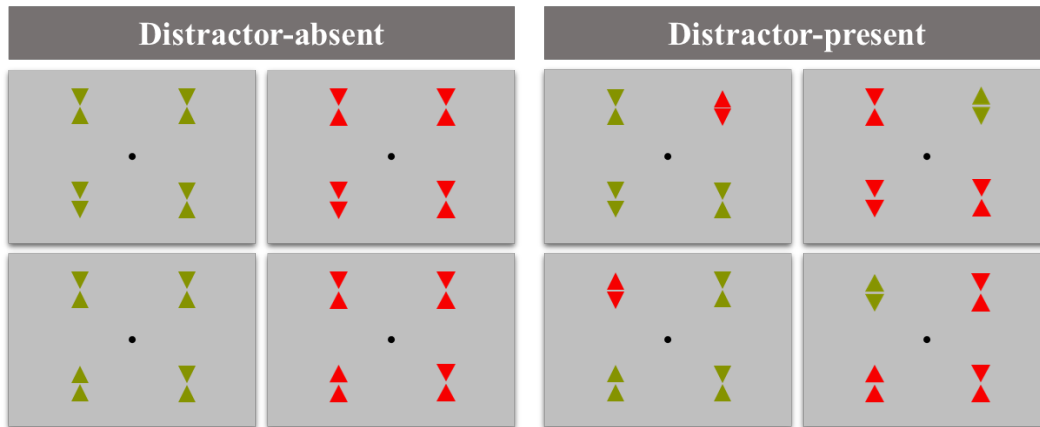


Figure 7. Displays of distractor-absent and distractor-present condition.

condition, another placeholder was replaced by the singleton distractor. This array was presented for 50 ms, followed by a blank display until the participants responded or, in case of no response, for 2000 ms. The following trial started after a 4000 ms intertrial interval (Figure 8).

Participants were asked to quickly and accurately identify the orientation of triangles (either “up” or “down”) of the target stimulus in the experiment, by pressing “1” or “2” on the keyboard (“1” for “up” and “2” for “down” or vice versa, counterbalanced across participants). The experiment was held in two sessions, one per day, with a practice block of 24 trials included in each session to help participants become familiar with the task. There were a total of six experimental blocks, with three blocks for each TMS condition.

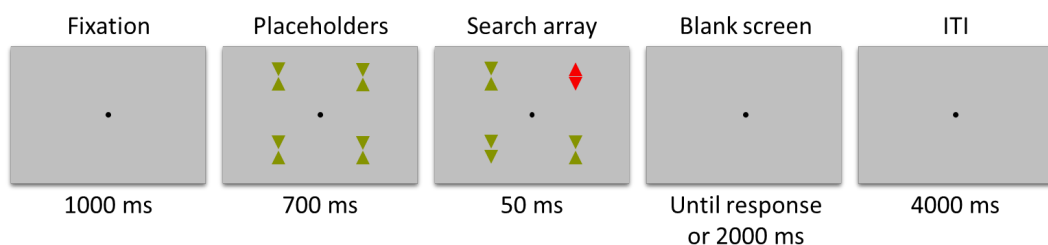


Figure 8. Schematic representation of temporal sequence of the experimental task.

Each block was composed of 72 trials, 36 of which were distractor-absent and 36 distractor-present, for a total of 432 trials per session, and 864 trials for the whole experiment. Both target and singleton distractor were presented with equal probability at any given spatial location. The order of the blocks was pseudo-randomized. The sessions were identical, except that the order of the blocks in the second session was reversed relative to the first one, to reduce any carryover effects related to the stimulation site. Each experimental session lasted ~2h.

TMS Online neuro-navigated TMS was delivered by means of a Magstim Super Rapid2 stimulator via a 70-mm figure-of-eight coil (Magstim Company, Whitland, UK). Before the experiment, the individual resting motor threshold (rMT) for the right first dorsal interosseous (FDI) was measured. First, the optimal coil position over the left motor cortex to induce a muscular twitch was determined; second, the initial supra-threshold intensity of TMS was progressively reduced in order to achieve the rMT, defined as the lowest intensity of the stimulator output which was capable of inducing five motor-evoked potentials (MEPs) with an amplitude of at least 50 μ V in a series of 10 consecutive impulses in the target muscle (Rossini et al., 1994). MEPs were recorded with 10-mm g/AgCl surface cup electrodes. The active electrode was placed over the FDI muscle of the right hand and the reference electrode over the metacarpophalangeal joint of the index finger. The electromyographic signal was amplified (D360 8-channel amplifier, Digitimer Ltd, Welwyn Garden City, Hertfordshire, UK), digitized (5000 Hz, CED Power 1401, Cambridge Electronic Design, Cambridge, UK), band-pass filtered (2–2000 Hz) and fed into a data acquisition system (Spike2 Version 7 for Windows, Cambridge Electronic Design, Cambridge, UK) for online visualization during the rMT estimation.

During the experiment, TMS was delivered at 120% of the individual rMT (mean intensity = 67.19% of the maximum stimulator output) over one active and one sham stimulation site. Both active and sham sites were right FEF. In the active stimulation condition, the coil was initially placed over the site with an

orientation of $\sim 45^\circ$ from the nasion-inion line with the handle pointing outwards and then adjusted for each participant to ensure the minimum discomfort. For the sham condition, the coil was held perpendicular to the scalp in order to avoid the stimulation while maintaining auditory and least some somatosensory correlates of active TMS. Since the aim of the study was to investigate the temporal dynamics of distractor suppression and target selection within the same brain architecture, a single TMS pulse was delivered over the right FEF at different time points relative to display onset. Precisely, TMS could be delivered 50, 200 or 350 ms after the onset of the search array to cover the same time window crucial for attentional capture and distractor suppression, as in Lega et al., (2019) (Figure 10).

TMS was delivered with equal probability at any given temporal point. Therefore, there were a total of 288 trials with TMS delivered at 50 ms, 288 trials with TMS at 200 ms and 288 trials with TMS at 350 ms. The experiment was divided into two sessions, each comprising six experimental blocks - three for each TMS condition. The order of these blocks was pseudo-randomized to avoid biases. Notably, the sessions were identical, except for the reversed order of blocks in the second session relative to the first one. This sequencing adjustment aimed to minimize any potential carryover effects associated with the stimulation site. Consequently, right FEF was stimulated at 50 ms, 200 ms, and 350 ms in 144 trials each, and the sham site received TMS at the same time points in an analogous manner.

Statistical analysis All the statistical analyses were performed using R (R Development Core Team, 2016). RTs were log-transformed to overcome deviations from normality (before transformation: skewness = 1.75; kurtosis = 4.38; after transformation: skewness = 0.57, kurtosis = 0.5). Only correct-response trials were included in the analyses. We used linear mixed-effects models as the main statistical procedure (Baayen et al., 2008), including in each model the

maximal random-effects structure (Barr et al., 2013). To estimate the models, we used the *lme4* package; to perform *post-hoc* tests, the *phia* package with Bonferroni-Holm correction was used. When a significant effect was found, effect size was calculated as Cohen's f^2 (Selya et al., 2012), which uses residual variance from the model to estimate effect size. The analysis of variance in the data was conducted using mixed-effects models and two different R^2 measures were obtained: the marginal R^2 , which provides an indication of the variance accounted for by the fixed effects, and the conditional R^2 , which measures the variance accounted for by the entire model. As a result, two different f^2 measures were calculated: the marginal f_m^2 and the conditional f_c^2 . Following Cohen's (1988) criteria, effect sizes of $f^2 \geq 0.02$, $f^2 \geq 0.15$, and $f^2 \geq 0.35$ are indicative of small, medium, and large effects, respectively.

2. Results

In this study, the impact of TMS on performance was measured using a linear mixed-effect model. The model was utilized to predict response times in correct trials, taking into account various factors such as TMS condition (right FEF vs. sham), pulse timing (50 ms, 200 ms, or 350 ms), the presence or absence of distractors, and all interactions between these factors. The model also included random coefficients across participants for the intercept and each of the factors. The analysis (Figure 11) revealed a significant main effect of distractor presence ($F_{(1,29.1)} = 277.5$, $p < 0.001$, $f_m^2 = 0.067$, $f_c^2 = 0.078$), pulse time ($F_{(12,39.7)} = 16.77$, $p < 0.001$, $f_m^2 = 0.005$, $f_c^2 = 0.006$), and a significant interaction between distractor presence and pulse time ($F_{(2,23622)} = 7.01$, $p < 0.001$, $f_m^2 = 0.0003$, $f_c^2 = 0.002$). Experiencing a salient but task-irrelevant distractor in the current trial increased RTs (614.69 ms), relative to the distractor-absent condition (515.93 ms). The main effect of pulse time might be attributed to the somatosensory correlates of the stimulation. Despite the auditory isolation measures implemented for participants, these somatosensory correlates acted as supplementary distractors,

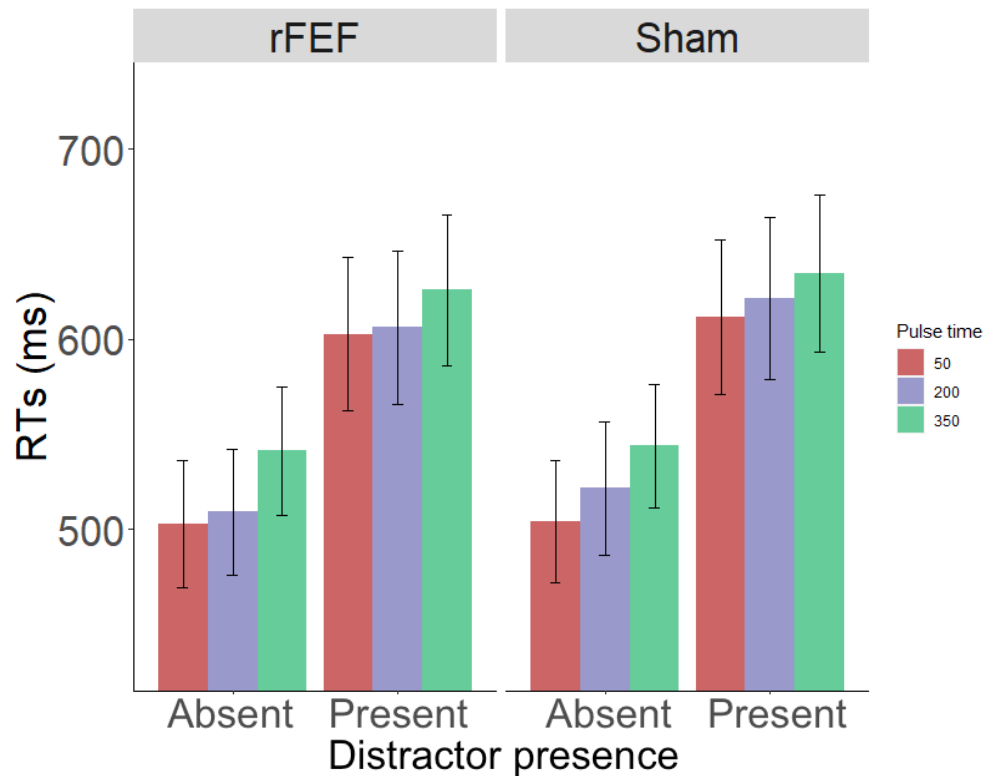


Figure 11. Mean RTs in the absence and presence of a salient distractor in active (right FEF) and sham TMS stimulations across the three timings conditions.

leading to a progressive delay in RTs, with the delay becoming more pronounced as the TMS pulse was administered later within the trial (50 ms pulse time: 553.98 ms; 200 ms pulse time: 563.2 ms; 350 ms pulse time: 586.47 ms). We did not find any significant main effect or interactions of TMS, but just a quasi-significant main effect of such factor ($F(1,28.6) = 3.6, p = 0.069$), that indicates a slight decrease of RTs when TMS was delivered over right FEF (563.32 ms) relative to sham condition (571.7 ms). To further explore the quasi-significant effect of TMS over behavior, two separate analyses were conducted for trials with and without distractors. The analysis of distractor-absent trials revealed only a significant effect of pulse time ($F(2,41.9) = 19.41, p < 0.001$), whereas the analysis of distractor-present trials showed a main effect of pulse time ($F(2,32.9) = 9.82, p = 0.004$) and a nearly significant effect of TMS ($F(1, 27.9) = 4.15, p = 0.051$), indicating a small reduction of RTs when TMS was delivered over right FEF (611.3 ms) relative to the sham condition (622.26 ms), only in distractor-present trials.

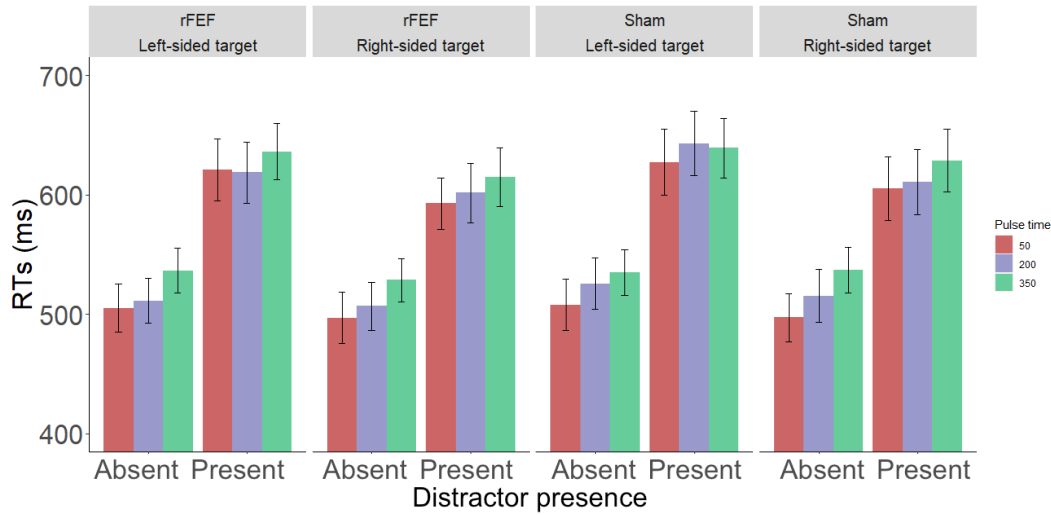


Figure 12. Mean RTs in distractor-absent and distractor-present conditions, splitted by TMS, target location and pulse time conditions.

We investigated a possible lateralized effect of TMS with a model that also included target location (left vs right). The analysis (Figure 12) revealed a significant main effect of distractor presence ($F_{(1,30.1)} = 288.1, p < 0.001, f^2_m = 0.067, f^2_c = 0.08$), target location ($F_{(1,29.8)} = 17.46, p = 0.0002, f^2_m = 0.002, f^2_c = 0.004$) and pulse time ($F_{(2,41.6)} = 17.1, p < 0.001, f^2_m = 0.005, f^2_c = 0.006$), and a significant interaction between distractor presence and target location ($F_{(1,23603)} = 16.56, p < 0.001, f^2_m = 0.004, f^2_c = 0.005$) and between distractor presence and pulse time ($F_{(2,23602)} = 7.16, p < 0.001, f^2_m < 0.001, f^2_c = -0.0001$), but again no significant effects of TMS were found.

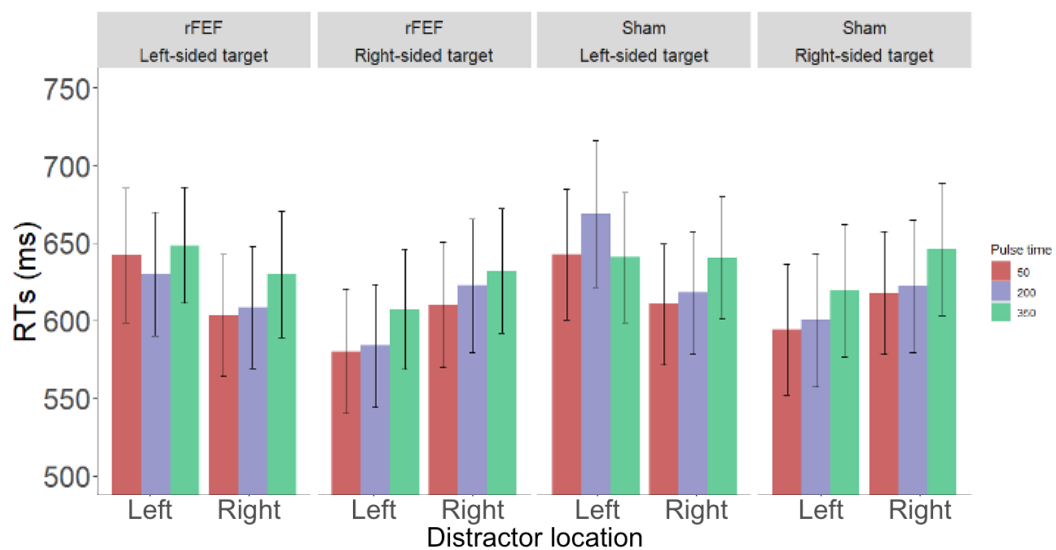


Figure 13. Mean RTs in the distractor-present trials, splitted by TMS, target location, distractor location and pulse time conditions.

We assessed a possible lateralized effect of TMS also for distractor location (left vs right), with a linear mixed-effect model that predicted RTs in only distractor-present trials (Figure 13). The analysis revealed a significant main effect of pulse time ($F_{(1,30.2)} = 7.3, p = 0.003, f_m^2 = 0.003, f_c^2 = 0.0045$) and target location ($F_{(1,11537)} = 57.32, p < 0.001, f_m^2 = 0.003, f_c^2 = 0.006$), and a significant interaction between target location and distractor location ($F_{(1,11537)} = 72.57, p < 0.001, f_m^2 = 0.004, f_c^2 = 0.004$), but again no significant effects of TMS were found.

Further analyses were performed over the distractor cost, i.e., the difference in RTs between distractor-present and distractor-absent trials. TMS (right FEF vs sham), pulse time (50 vs 200 vs 350), along with all their interactions were included as fixed effects. Random coefficients were estimated for each participant in terms of intercept and the aforementioned factors. The analyses (Figure 14) showed only a main effect of pulse time ($F_{(2,34.74)} = 6.001, p = 0.006, f_m^2 = 0.035, f_c^2 = 0.16$). Experiencing the somatosensory correlates of stimulation led to a marginal reduction in the distractor cost, particularly evident when the TMS

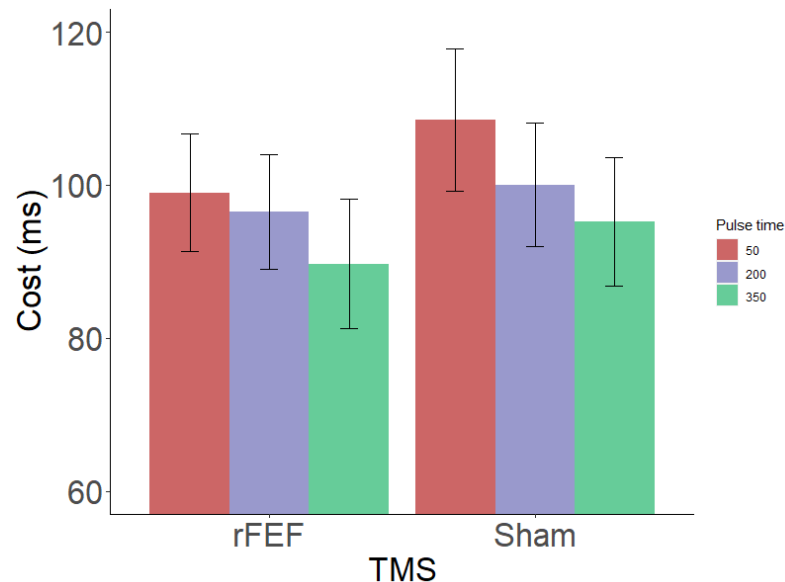


Figure 14. Mean distractor cost (RTs) over active (right FEF) and sham stimulation in all the three timing conditions.

pulse was administered at later time intervals (50 ms = 103.75 ms; 200 ms = 98.25 ms; 350 ms = 92.15 ms). It's important to note that this outcome might appear contradictory to the results presented in Figure 11, where the somatosensory correlates were associated with increased RTs as the TMS pulse was delayed. However, this discrepancy can be attributed to the nature of the distractor cost analysis, which reflects the RT difference between trials with and without distractors. Particularly, the distractor absent condition seems to be more negatively impacted by the somatosensory disturbance, relative to the distractor present one. One possible explanation for this phenomenon could be that the absence of a distractor magnifies the impact of the somatosensory disruption, whereas in the presence of a distractor, such influence is potentially "masked" by the attention-grabbing yet irrelevant visual distraction.

Again, we assessed a possible lateralization effect of the TMS by including to the model (Figure 15) also target location (left vs right), and distractor location (left vs right). We found a main effect of pulse time ($F(2,629.99) = 11.81, p < 0.001, f^2_m = 0.02, f^2_c = 0.05$), distractor location ($F(1,30.27) = 15.88, p < 0.001, f^2_m = 0.05, f^2_c = -0.005$) and an interaction between target location and distractor location ($F(1,692.99) = 33.68, p < 0.001, f^2_m = 0.03, f^2_c = 0.04$), but no main effect or interaction of TMS.

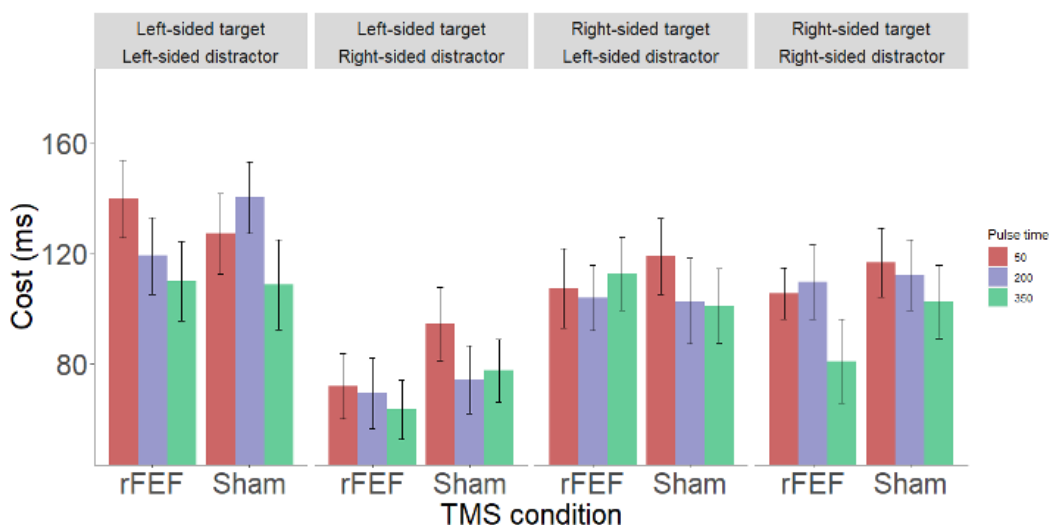


Figure 15. Mean distractor cost (RTs) over active (right FEF) and sham stimulation, splitted by target location, distractor location and all three timing conditions.

3. Discussion

The goal of Experiment 1 was to gain insight into the temporal dynamics of the neural mechanisms involved in selecting relevant information and ignoring irrelevant distractions, specifically within the right FEF. This region of the brain was found to be critical in a prior study (Lega et al., 2019) and was investigated using a time-punctate single-pulse TMS approach, with stimulation delivered at three different time points (50, 250, and 350 ms after the search array onset). The aim of this temporal analysis was to determine whether the positive effect of triple-pulse, 10 Hz, TMS stimulation of the right FEF on distractor cost was due to an enhancement of the ability to counteract the distractions caused by salient but irrelevant stimuli or to a disruption of the computation of the salience of these distracting items, leading to reduced attentional capture. To identify the source of the improved performance, single-pulse TMS was delivered at the same stimulation points as used by Lega et al. (2019) within the same stimulation window.

However, the results of Experiment 1 were surprising in that no significant effect of TMS on distractor suppression was found, in contrast to the evidence presented in the work of Lega and colleagues (2019), which highlighted the importance of the right FEF in filtering out salient distractions. Instead, the results of Experiment 1 showed only a general, time-unspecific, and quasi-significant effect of TMS, resulting in faster reaction times when TMS was delivered over the right FEF compared to the sham condition. It is noteworthy that despite using the same time window as the prior study, the use of single-pulse stimulation on the right FEF was not sufficient to produce the same behavioral effects as the 10 Hz triple-pulse stimulation applied in the above-mentioned study. The quasi-significant effect of TMS over behavior seems to suggest that TMS applied to the right FEF may have had a slightly positive impact on attentional processes in the visual search task. Particularly, this facilitation could be related to the mechanism of target selection, as it appears to be present in both the distractor-absent and

distractor-present conditions. However, it is important to note that these findings are based on nearly significant results, and further research is needed to fully understand the effect of this type of TMS protocol on the right FEF and its role in distractor suppression.

Additionally, it is worth noting that the stimulation protocols used in the two experiments, although within the same temporal window, exhibited crucial differences. In Lega et al. (2019), stimulation was administered as a triple-pulse burst at a frequency of 10 Hz, while in Experiment 1, it consisted of a single pulse delivered once per trial at one of the three time points (50 ms, 250 ms, and 350 ms). The reason why the results of Experiment 1 did not replicate those of Lega et al. (2019) may stem from the distinct physiological effects induced by these differing stimulation protocols on the right FEF. Specifically, in Lega et al. (2019) the 10 Hz triple-pulse stimulation may have influenced the rhythmic neural patterns associated with attentional deployment, through an entrainment effect in the alpha band driven by the right FEF stimulation. Several TMS-EEG studies have suggested that the right FEF plays a role in biasing electrical activity in posterior brain regions (Sauseng et al., 2011; Capotosto et al., 2009; Taylor et al., 2006). Taking this evidence into account, along with the well-established connection between alpha power and attentional modulation (Kastner and Ungerleider, 2000; Corbetta and Shulman, 2002; Worden et al., 2000; Serences and Yantis, 2006; Moore et al., 2003; Bressler et al., 2008; Fries, 2005; Engel et al., 2001; Steriade and Llinas, 1988; Klimesch et al., 1998; Sauseng et al., 2005; Thut et al., 2006), it's plausible that the 10 Hz TMS applied in Lega et al. (2019) boosted posterior alpha power, leading to improved filtering of distractors. Conversely, the single-pulse TMS used in Experiment 1 might not have generated the same entrainment effect due to its non-rhythmic, isolated nature. As a result, Experiment 1 exhibited the observed quasi-significant facilitation of attentional processes, albeit without the specific focus on distractor suppression mechanisms seen in Lega et al. (2019). While this hypothesis offers a potential explanation for the variance in outcomes between the two studies, further research is essential to

fully elucidate the intricate effects of TMS-induced entrainment on attentional control mechanisms.

2. Experiment 2

1. Methods

Participants 30 healthy naïve participants (mean age = 23.77, $SD = 3.52$, 27 females) were tested. All participants were right-handed and with normal or corrected-to-normal vision. Before the TMS experiment, all participants filled out a safety screening questionnaire (Rossi, Hallett, Rossini & Pasqual-Leone, 2009), to exclude possible contraindications to the TMS application. The study was approved by the local Ethics Committee (Department of Neuroscience, Biomedicine and Movement Sciences, University of Verona) and conducted in accordance with the Declaration of Helsinki. Informed consent was obtained from all individual participants included in the study.

Materials and stimuli The paradigm was identical to Experiment 1.

Procedure The procedure was identical to Experiment 1.

TMS. Here we used the same neuro-navigated TMS approach as in Experiment 1, with some crucial differences in the stimulation protocol. During the experiment, TMS was delivered at 100% of the individual rMT (mean intensity = 53.7% of the maximum stimulator output) over one active and one sham stimulation site. Both active and sham sites were right FEF. In the active stimulation condition, the coil was initially placed over the site with an orientation of $\sim 45^\circ$ from the nasion-inion line with the handle pointing outwards and then adjusted for each participant to ensure the minimum discomfort. For the sham condition, the coil was held perpendicular to the scalp in order to avoid the stimulation while maintaining auditory and at least some of the somatosensory correlates of active TMS. Since the aim of the study was to further investigate the temporal dynamics of distractor suppression and target selection within the same brain architecture, a triple-pulse stimulation at 20 Hz was delivered at different time points across the experiment (Figure 16). Triple-pulse TMS could be delivered to have the last pulse at 50 (T1), 200 (T2), or 350 (T3) ms after the

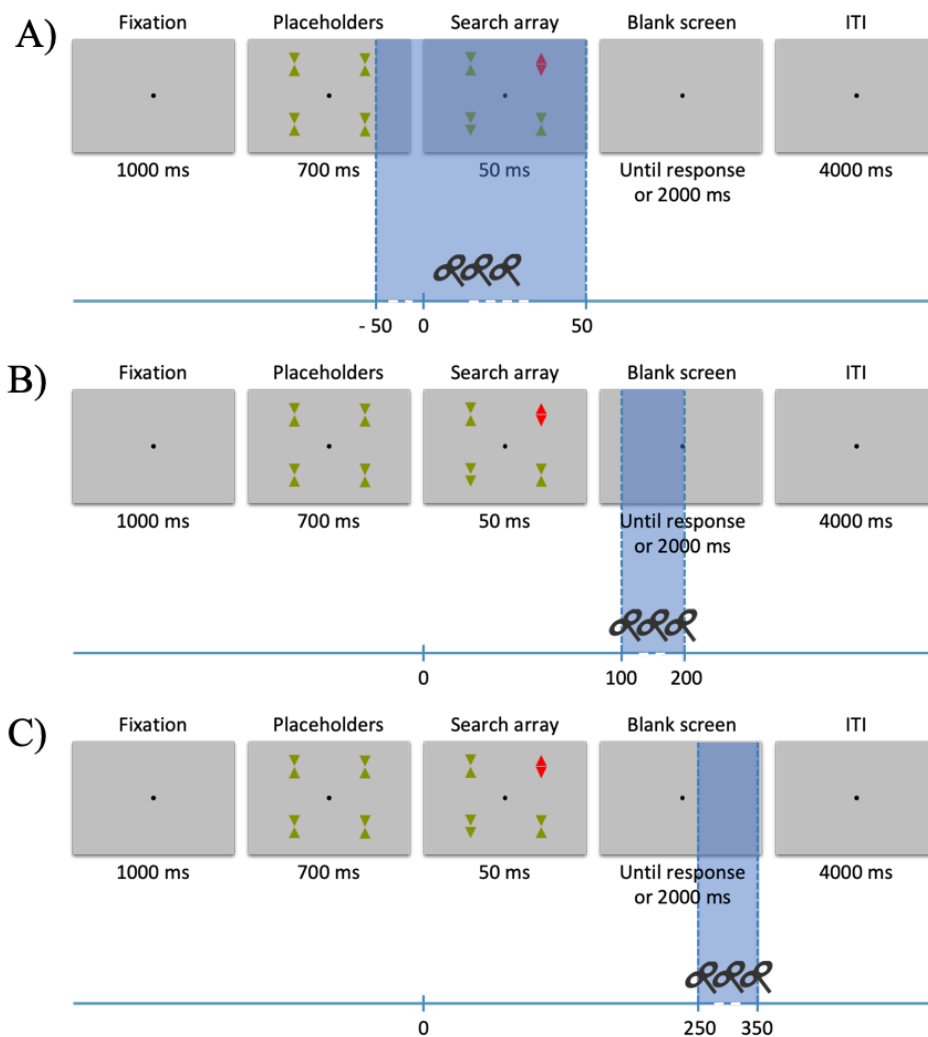


Figure 16. Schematic representation of stimulation timing during the task. A) TMS delivered at T1 covered a time window from -50 to 50 ms after the search array onset; B) TMS delivered at T2 covered a time window from 100 to 200 ms after the search array onset; C) TMS delivered at T3 covered a time window from 250 to 350 ms after the search array onset.

onset of the search array. Precisely, the T1 time condition covered a time window between -50 to 50 ms, T2 from 100 to 200 ms, and T3 from 250 to 350 ms. The stimulation protocol of Experiment 2 had two main objectives: first, a triple-pulse stimulation was applied in the attempt to achieve a stronger impact on the right

FEF brain tissue, with the TMS trains culminating at the same time points as the single-pulse TMS used in Experiment 1; second, the frequency of stimulation was set to 20 Hz, differing from the 10 Hz used in the study by Lega and colleagues (2019), to explore whether the effect observed in their study was a result of this precise rhythm of stimulation on the right FEF. TMS was delivered with equal probability at any given temporal window. Therefore, there were 288 trials with TMS delivered at T1, 288 trials with TMS at T2, and 288 trials with TMS at T3. The experiment was divided into two sessions, each comprising six experimental blocks - three for each TMS condition. The order of these blocks was pseudo-randomized to avoid biases. Notably, the sessions were identical, except for the reversed order of blocks in the second session relative to the first one. This sequencing adjustment aimed to minimize any potential carryover effects associated with the stimulation site. Consequently, right FEF was stimulated at T1, T2, and T3 in 144 trials each, and the sham site received TMS at the same time points in an analogous manner.

Statistical analysis. In the present study were performed the same statistical analyses as in Experiment 1. RTs were log-transformed to overcome deviations from normality (before transformation: skewness = 1.82; kurtosis = 4.57; after transformation: skewness = 0.64, kurtosis = 0.55).

2. Results

In this study, the impact of TMS on performance was measured using a linear mixed-effect model. The model was utilized to predict response times in correct trials, taking into account various factors such as TMS condition (right FEF vs. sham), time (T1 vs. T2 vs. T3), the presence or absence of distractors, and all interactions between these factors. The model also included random coefficients across participants for the intercept and each of the factors. The analysis (Figure 17) revealed a significant main effect of distractor presence ($F(1,28.7) = 354.5, p < 0.001, f_m^2 = 0.07, f_c^2 = 0.08$) and time ($F(2,28.8) = 38.94, p < 0.0001, f_m^2 = 0.005, f_c^2 = 0.005$), and a significant interaction between distractor presence and time ($F(2,23688.9) = 15.31, p < 0.0001, f_m^2 = 0.0008, f_c^2 = 0.0007$). Consistently with the previous experiment, encountering a salient but task-irrelevant stimulus was associated with slower RTs (mean 654.11 ms) relative to the distractor-absent condition (mean 545.95 ms).

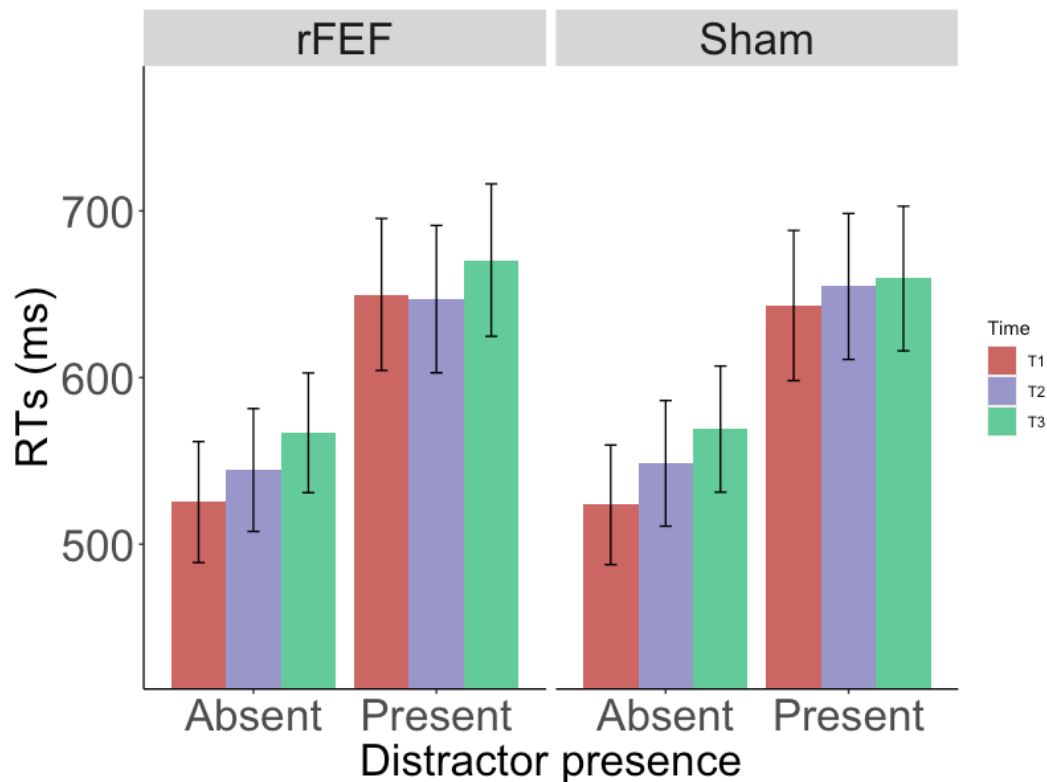


Figure 17. Mean RTs in the absence and presence of a salient distractor in active (right FEF) and sham TMS stimulations across the three timings conditions.

Similar to Experiment 1, we observed the disrupting influence of the somatosensory correlates of the stimulation over the RTs. This disruption was most pronounced as the TMS train was delivered later in time, potentially interfering with the mechanisms responsible for suppressing distractors during the task (T1: 122.24 ms; T2: 105.44 ms; T3: 100.26 ms). We did not find any significant main effect or interaction of the TMS condition.

We investigated an eventual lateralized effect of TMS by including also target location (left vs right) in the model. The analyses (Figure 18) showed a significant main effect of distractor presence ($F(1,29.7) = 372.9, p < 0.001, f_m = 0.074, f_c = 0.08$) and a significant interaction between distractor presence and target location ($F(1,23709.4) = 13.5, p < 0.001, f_m = 0.0005, f_c = 0.0003$), and between distractor presence and time ($F(1,23696.5) = 15.32, p < 0.001, f_m < 0.001, f_c < 0.001$), but again no significant main effect or interaction of TMS condition was found.

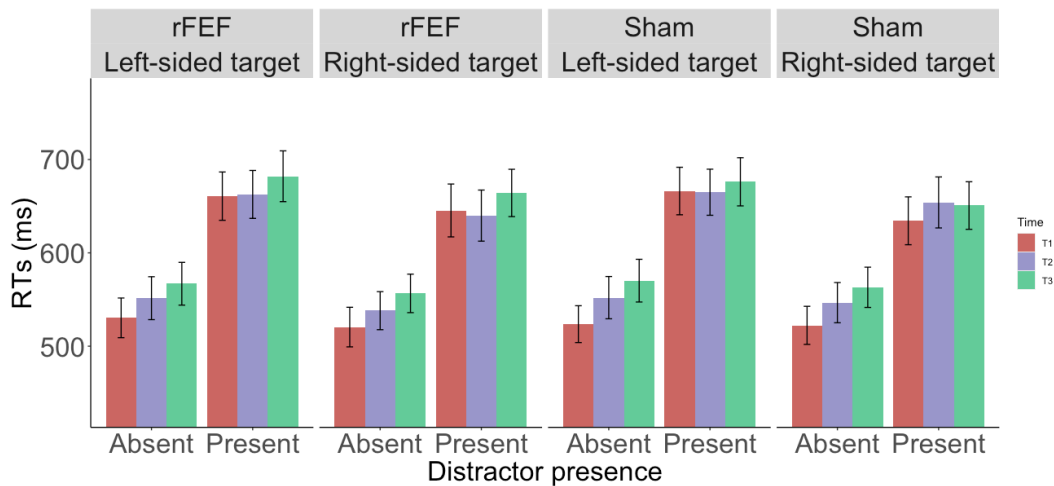


Figure 18. Mean RTs in distraction-absent and distractor-present trials, splitted by TMS, target location and time conditions.

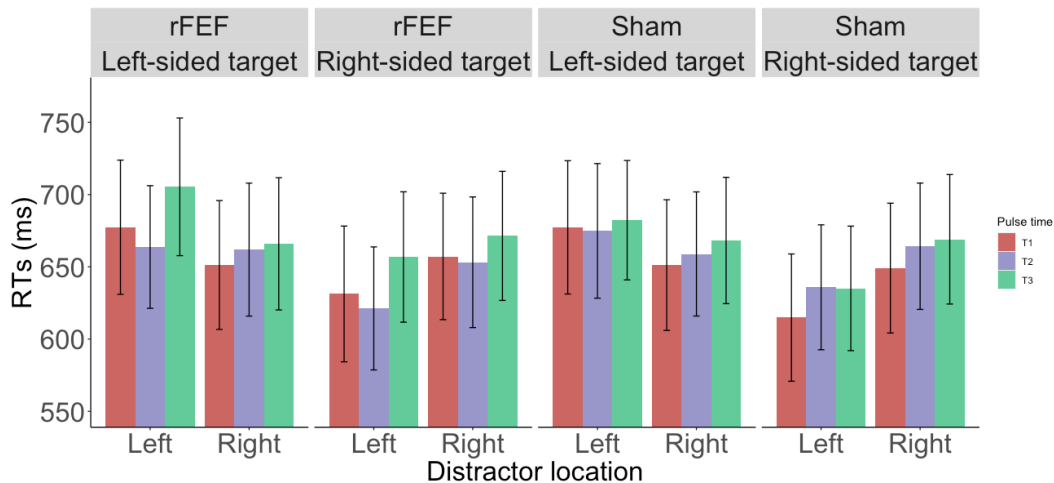


Figure 19. Mean RTs in the distractor-present trials, splitted by TMS, target location, distractor location and time conditions.

Further analyses were performed including also distractor location (left vs right) in a model that predicted RTs only in distractor-present trials (Figure 19). Here we found a significant main effect of time ($F(2,33.7) = 7.84, p = 0.002, f_m^2 = 0.002, f_c^2 = 0.004$), target location ($F(1,30.4) = 6.81, p = 0.02, f_m^2 = 0.002, f_c^2 = 0.01$) and a significant interaction between target location and distractor location ($F(1,11369.6) = 45.97, p < 0.001, f_m^2 = 0.003, f_c^2 = 0.002$), reflecting increased RTs when target and distractor were displayed on the same side (mean 670.44 ms) relative to different ones (mean 645.99 ms). This analysis did not reveal any main effect or interaction of TMS.

We assessed the effect of TMS (right FEF vs sham) and time (T1 vs T2 vs T3) over the distractor cost, i.e. the difference in RTs between distractor-present and distractor-absent trials. The analyses (Figure 20) revealed only a significant main effect of time ($F(2,36.11) = 11.9, p < 0.001, f_m^2 = 0.08, f_c^2 = 0.23$). Similar to the findings observed in Experiment 1, experiencing the somatosensory correlates of stimulation led to a marginal reduction in the distractor cost, particularly evident when the TMS pulse was administered at later time intervals (T1 = 122.24 ms; T2 = 105.44 ms; T3 = 100.26 ms).

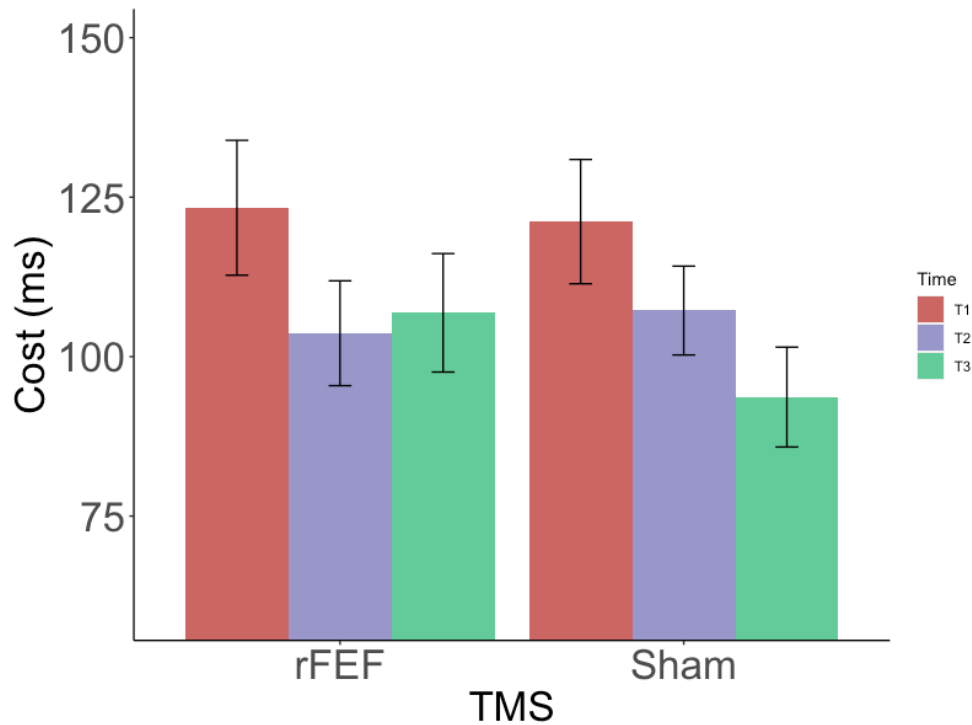


Figure 20. Mean distractor cost (RTs) over active (right FEF) and sham stimulation in all the three timing conditions.

Again, we investigated a possible lateralization effect of the TMS including both target and distractor locations (left vs right) in the model (Figure 21). Here we found a significant main effect of time ($F(2,32.7) = 13.19, p < 0.001, f^2_m = 0.03, f^2_c = 0.07$) and distractor location ($F(1,30) = 6.5; p = 0.02; f^2_m = 0.05; f^2_c = -0.005$), a significant interaction between target location and distractor location ($F(1,569.6) = 34.17, p < 0.001, f^2_m = 0.027, f^2_c = 0.03$), and an interesting nearly-significant three-way interaction between time, TMS and distractor location ($F(2,569.86) = 2.65, p = 0.07$). Post-hoc analyses (Figure 22) revealed an increased distractor cost, selectively for distractors located contralaterally to the stimulation site, when TMS was applied at T2 over right FEF (mean 130.5 ms; $t = 2.19, p = 0.036$) relative to the sham condition (mean 108.3 ms).



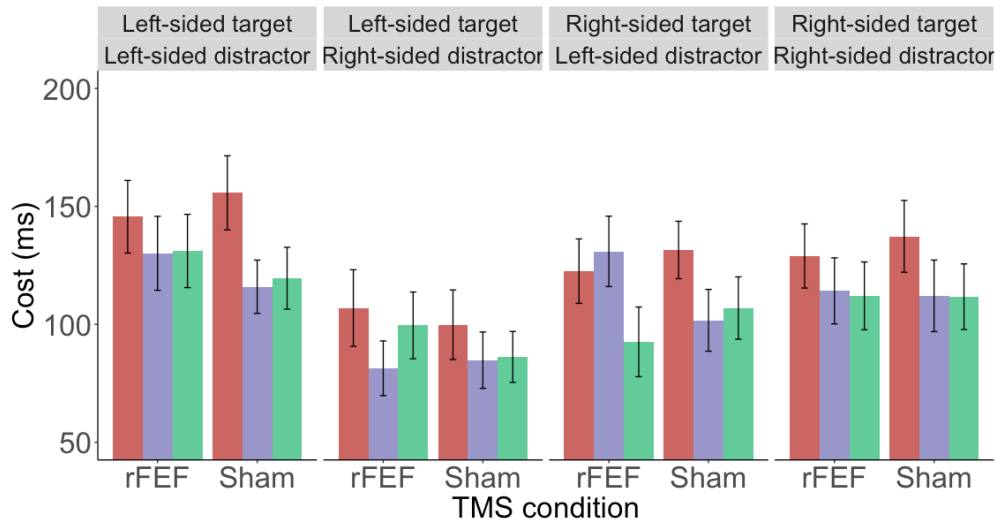


Figure 21. Mean distractor cost (RTs) over active (right FEF) and sham stimulation in all three timing conditions. TMS over right FEF delivered at T2 (100-200 ms after search array onset) selectively reduced distractor cost only

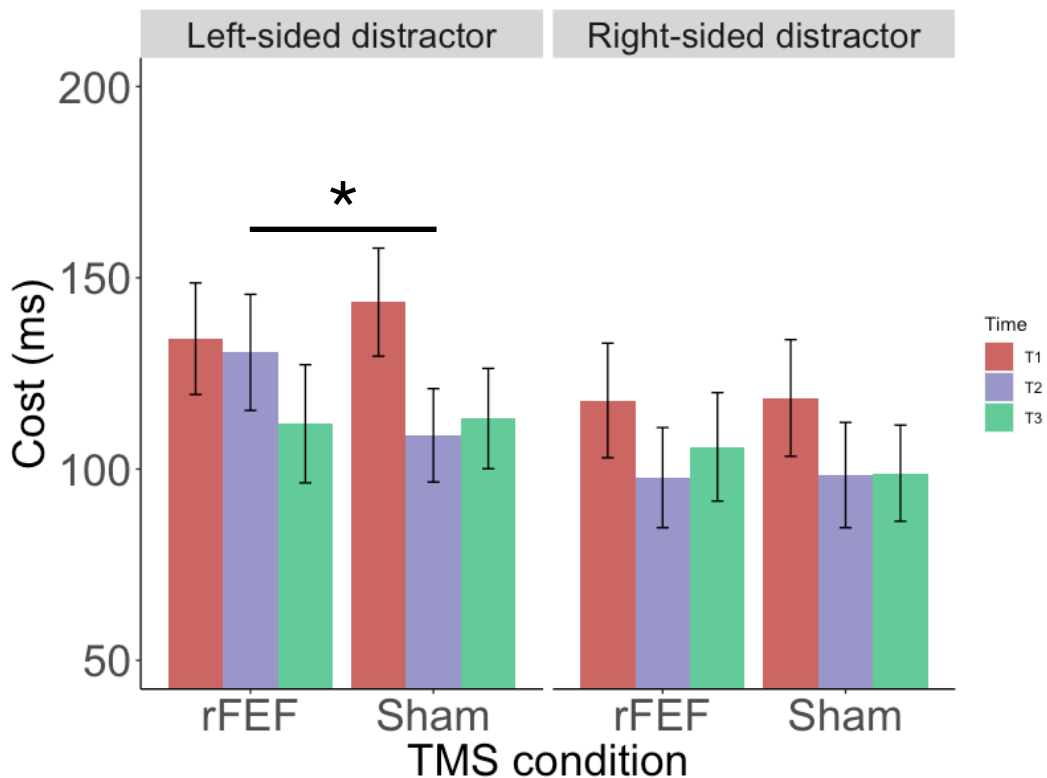


Figure 22 - Mean distractor cost (RTs) over active (right FEF) and sham stimulation in all three timing conditions, splitted by only distractor location. TMS over right FEF delivered at T2 (100-200 ms after search array onset) selectively reduced distractor cost only for distractors located contralaterally to the stimulation site.

3. Discussion

Experiment 2 aimed to examine the temporal dynamics of the neural mechanisms that control the selection of relevant information and the suppression of irrelevant distractions, specifically within the right Frontal Eye Field (FEF). Previous research has identified this region of the brain as critical for these processes (Lega et al., 2019). To achieve this aim, a time-punctate triple-pulse TMS approach was used, in which stimulation was delivered at three different time windows after the onset of the search array (T1: -50 ms to 50 ms; T2: 100 ms to 200 ms; T3: 250 ms to 350 ms). As in Experiment 1, the aim of this temporal analysis was to determine whether the positive effect of triple-pulse, 10 Hz, TMS stimulation of the right FEF on distractor cost was due to an enhancement of the ability to counteract the distractions caused by salient but irrelevant stimuli or to a disruption of the computation of the salience of these distracting items, leading to reduced attentional capture. To identify the source of the improved performance, triple-pulse, 20 Hz, TMS was applied within the same stimulation window as in Lega et al., (2019). The stimulation protocol in Experiment 2 was specifically designed to enhance the effects of TMS over the right FEF. To achieve this, the experiment used a triple-pulse stimulation, as opposed to the single-pulse approach used in Experiment 1. The single-pulse TMS used in Experiment 1, delivered at 50, 200, or 350 ms, was not effective in inducing any behavioral effect. Therefore, in Experiment 2, the triple-pulse stimulation was administered with the last pulse delivered at the same time points as the single-pulse stimulation in Experiment 1, in an attempt to exert a stronger influence on the right FEF and clarify its contribution to target selection and distractor suppression.

According to our expectations, the results of Experiment 2 showed a quasi-significant effect of TMS over behavior. The use of a triple-pulse, 20 Hz, TMS allowed for an increased impact of the stimulation on the right FEF, as compared to the single-pulse protocol used in Experiment 1. Experiment 2 showed an interesting time-specific and also spatial-specific effect: TMS over the right FEF

was found to have a negative effect on distractor cost, particularly when applied at T2 (100-200 ms after the onset of the search array) with the distractor located contralaterally to the stimulation site. This result, although only in a precise spatial configuration, supports the findings of Lega et al. (2019) and suggests that the right FEF plays a role in filtering out salient yet task-irrelevant distracting stimuli. Particularly, the negative effect at T2 allows for temporally circumscribing the finding in Lega et al., (2019) to a narrower time window, enabling us to clarify the source of benefit over distractor cost found in their study: triple-pulse, 10 Hz, TMS over right FEF empowered the distractor suppression mechanism, rather than weakened the salience computation leading to a dampened automatic capture by the salient distractor.

EEG evidence has shown that a specific pattern of ERP components is deployed when a distractor is present (Liesefeld et al., 2017). This pattern is characterized by an early distractor-related N2pc component (reflecting attention being automatically captured by the salient distractor) immediately followed by a Pd component (signaling the suppression of the elaboration of the salient distractor) and then by a final target-related N2pc component (reflecting the successful shifting of attention from the distractor to the target, and the subsequent selection of the target). Interestingly, when the target and distractor were located on opposite sides of the same display, the EEG amplitudes were initially more negative on the side contralateral to the distractor and later became more negative on the side contralateral to the target, indicating a shift in attention from the distractor to the target (*N2pc flip*; Liesefeld et al., 2017). The latency difference between the distractor and target N2pc components (~117 ms) was consistent with previous estimates for the time required for attentional reallocation in visual search (100-150 ms; Woodman and Luck, 2003; Liesefeld et al., 2017). Considering these temporal dynamics, it is possible that the time-punctate TMS approach used in Experiment 2 has influenced the attentional mechanisms activated when a distractor was present.

In this regard, studies have shown that the interaction between regions in the dorsal frontoparietal cortex and occipital visual regions plays a role in shaping perception through spatial attention. The modulation of posterior alpha rhythms as recorded with EEG is a potential marker of this interaction, showing changes in power in response to visual stimulation and anticipation of visual targets. The topography of these alpha rhythms becomes spatially selective when subjects expect a target at a specific location, and can predict the locus of attention and visual performance. (Kastner and Ungerleider, 2000; Corbetta and Shulman, 2002; Worden et al., 2000; Serences and Yantis, 2006; Moore et al., 2003; Yamagishi et al., 2003; Ruff et al., 2006, 2008; Bressler et al., 2008; Fries, 2005; Engel et al., 2001; Steriade and Llinas, 1988; Klimesch et al., 1998; Sauseng et al., 2005; Thut et al., 2006). Interestingly, TMS-EEG studies suggested the right FEF plays a role in biasing electrical activity in posterior regions of the brain (Sauseng et al., 2011, Capotosto et al., 2009; Taylor et al, 2006). For instance, Capotosto and colleagues (2009) found that delivering 20 Hz repetitive TMS (rTMS) to the right FEF led to a disruption of the posterior alpha desynchronization activity in both hemispheres. Furthermore, Taylor et al. (2007) found that delivering 10 Hz rTMS to the right FEF led to an increase in negativity in the electrical activity recorded in the posterior areas, especially for the ipsilateral hemisphere, and such negativity amplitude was significant starting from the third pulse (i.e. 200 ms after the start of the stimulation). Therefore, it is possible that the stimulation of the right FEF at T2 (from 100 ms to 200 ms post-stimulus) in Experiment 2 may have modulated distractor suppression mechanisms rather than salience computation and attentional capture. This conclusion is supported by the fact that the T2 time window aligns better with the time course of the ERP component of distractor suppression (Pd) compared to the temporal deployment of (distractor) N2pc. Furthermore, in Experiment 2 the effect was spatially-specific, as the increase in distractor cost was observed only when the distractor was located contralaterally to the stimulation site, regardless of the target location. If the TMS effect had reflected a modulation of salience

computation, it would have impacted not only the contralateral distractor but also the contralateral target, in both distractor-absent and distractor-present conditions.

It is noteworthy that, despite the same stimulation window, the results of Lega and colleagues (2019) and of Experiment 2 were characterized by opposite trends. In fact, the first study showed improved filtering of salient distractors - resulting in a decrease in the distractor cost - while the second provides evidence for a worsening of this mechanism - resulting in an increase of the distractor cost. Furthermore, in Lega and colleagues (2019) work the TMS effect over distractor cost was agnostic of any spatial configuration, while the effect of Experiment 2 was specific to distractors located contralaterally to the stimulation site. This difference in results might be due to the difference in stimulation frequency (10 Hz vs. 20 Hz). The different frequency of TMS application may lead to different physiological effects, and thus different effects on behavior.

The posterior alpha suppression pattern plays a crucial role in the deployment of attention, and its pattern can be biased by TMS applied in frontal areas (Capotosto et al., 2009; Sauseng et al., 2011; Taylor et al., 2006). The alpha rhythm has been linked to the facilitation and suppression of neuronal activity, as seen in the enhancement of relevant information processing and suppression of irrelevant inputs. Decreases in alpha power have been associated with the enhancement of sensory processing from a specific location or modality (Adrian, 1944; Frey et al., 2014; Fu et al., 2001; Mazaheri et al., 2014; Bauer et al., 2012; Sauseng et al., 2005; Worden et al., 2000), while increases in alpha power have been linked to the suppression of irrelevant inputs (ElShafei et al., 2018; Wöstmann, Alavash & Obleser, 2019). Therefore, it is possible that stimulating the right FEF at two different frequencies in the same visual search task and in the same time window may have led to crucially different effects on posterior alpha activity. In support of this hypothesis, an interesting study by Thut and colleagues (2011) showed that the application of 5-pulse trains of rTMS at the alpha (10 Hz) frequency was effective in exerting an entrainment effect over a parietal alpha-

generator, resulting in an enhancement of alpha power, visible starting from the third pulse. Meanwhile, the work of Capotosto and colleagues (2009) showed not only that (20 Hz) rTMS over right FEF was able to impair the desynchronization patterns of anticipatory alpha activity, but also that this kind of stimulation led to a worsening of the performance when the attention was directed to the invalid location, or in other words in a situation where attention needed to be disengaged from the attended (invalid) location to be shifted to the unattended (valid) one. Taking into account these evidences, it is possible that the benefit effect over distractor filtering exerted by the stimulation at 10 Hz applied by Lega and colleagues (2019) resulted in an increase of the posterior alpha power, leading to a boosted distractor filtering mechanism. Conversely, the 20 Hz stimulation applied in Experiment 2 resulted in an interference with the suppression of salient distractors, potentially due to the disruption of the alpha rhythm and its power.

6. General discussion

The aim of my PhD project was to unveil the temporal dynamics of target selection and distractor suppression in one of the key nodes of the frontoparietal attention network: the Frontal Eye Field (FEF). In a previous study (Lega et al., 2019) the contribution of both the IPS and FEF to visuo-spatial attention was assessed using triple-pulse TMS delivered at a frequency of 10 Hz during a visual search task. The stimulation was delivered in a post-stimulus epoch from 100 to 300 ms, which is believed to be crucial for attentional processes in visual search (Jannati et al., 2013; McDonald et al., 2013; Liesefeld et al., 2017). The study showed that the application of this protocol of TMS was able to exert an effect over the behavior, by boosting the distractor suppression mechanisms, resulting in a reduction of the cost engendered by experiencing a salient but task-irrelevant distractor while looking for the target. My work focused on clarifying the temporal contribution of right FEF to distractor suppression, and discerning the nature of the improvement of the performance found by Lega and colleagues (2019) - whether it was due to an enhanced top-down suppression of the distraction or a weakening of the computation of the salience of the distractor, leading to less bottom-up attention capture.

In the attempt to answer this question, two experiments were conducted. Experiment 1 applied single-pulse TMS over right FEF in three different time points over this crucial post-stimulus epoch: 50, 200 or 350 ms after the search array onset. However, this experiment did not show a significant effect of TMS on behavior, but only a general, time-unspecific, and quasi-significant effect on reaction times, indicating a slight increase in speed of the responses compared to the control (sham) condition. In order to exert a stronger TMS effect over right FEF while maintaining this temporal-punctate approach, Experiment 2 applied trains of triple-pulse TMS at 20 Hz over right FEF, delivered in three different post-stimulus time windows: T1 from -50 to 50 ms, T2 from 100 to 200 ms, T3 from 250 to 350 ms. The goal was to have the last pulse of each train occur at the

exact same time point as the single-pulse of Experiment, thereby ensuring a stronger stimulation of the neuronal populations of the right FEF, while also temporally investigating its role into distractor suppression. As expected, Experiment 2 revealed an effect of the stimulation: TMS at T2 (100-200 ms) was associated with an increase of the distractor cost, specifically for distractors located contralaterally to the stimulation site.

Taken together, these evidences suggest the key role of right FEF to the deployment of top-down suppression of salient but task-irrelevant distractors, confirming the results of Lega et al., (2019) and temporally isolating the contribution of this frontal area to such attentional mechanism. These outcomes align with the well-established role of the frontoparietal attention network in regulating the responsiveness of visual cortex regions and provide support for the overarching hypothesis that the right hemisphere predominantly governs attentional control (Grosbras and Paus, 2003; Silvanto et al., 2006, 2009; Scolari et al., 2015; Moore and Armstrong, 2003; Noudoost et al., 2010; Baluch and Itti, 2011; Buschman and Kastner, 2015; Bisley and Goldberg, 2010; Corbetta et al., 2011; Marini et al., 2016). Especially within the frontoparietal regions, there is a substantial body of evidence supporting the role of right FEF in top-down regulation of attention (Ruff et al., 2008; Hung et al., 2011; Serences et al., 2005; Natale et al., 2010; Moore & Fallah, 2004; O’Shea et al., 2004; Thompson et al., 2005; Buschman & Miller, 2007; Zhou & Thompson, 2009; Ronconi et al., 2014; Vossel et al., 2012; DiQuattro et al., 2013). Suppression mechanisms are believed to be carried out through prefrontal regulation of sensory processing (Serences et al., 2004; Gazzaley et al., 2007; Seidl et al., 2012; ElShafei et al., 2018; Wöstmann, Alavash & Obleser, 2019), similar to the enhancement of target features (Reynolds and Chelazzi, 2004; Chelazzi et al., 2011; Adrian, 1944; Frey et al., 2014; Fu et al., 2001; Mazaheri et al., 2014; Bauer et al., 2012; Sauseng et al., 2005; Worden et al., 2000). Several studies (Capotosto et al., 2009; Michalareas et al., 2016; Sauseng et al., 2011; Popov et al., 2017; Taylor et al., 2006; Wang et al., 2016) suggest that the right FEF can exert top-down control by

modifying visual alpha-band oscillatory activity in sensory areas. Interestingly, Popov et al. (2017) utilized MEG to show that only the right FEF has the ability to exert top-down control over visual cortex stimulus processing. This hemispheric asymmetry in the FEF supports the current findings and is further supported by the commonly observed effect of TMS on visual task performance in both hemifields when applied to the right FEF, and only in the right hemifield when applied to the left FEF (Smith et al., 2005; Grosbras and Paus, 2003; Silvanto et al., 2006). The results are consistent with the extensive literature suggesting the FEF in the right hemisphere is largely responsible for controlling visuo-spatial attention (Grosbras and Paus, 2003; Silvanto et al., 2006; Capotosto et al., 2009; Duecker et al., 2013; Marshall et al., 2015; Wang et al., 2016).

In conclusion, the present findings support the pivotal role of the right FEF in mitigating the impact of distractions from salient but irrelevant stimuli. Our results suggest that the TMS intervention activated the neural network that regulates and limits interference from these distractions, potentially by enhancing (as in Lega et al., 2019) or reducing (as in Experiment 2) the activity in posterior areas by means of different protocols of rTMS. Further research is needed to better understand the physiological effects of 10 Hz vs 20 Hz stimulation of the right FEF over the posterior regions, to gain insight into the mechanisms by which the frontal lobe is able to shape the activity over sensory areas by the deployment of visuo-spatial attention. Additionally, it remains to be determined whether the lack of TMS effect over IPS in the study of Lega et al., (2019) is due to an unsuitability of the 10 Hz protocol, or to the difficulty of the stimulation to exert an effect over the area due to its deep location in the intraparietal sulcus, or again to the limitations of the chosen post-stimulus time epoch in tapping on the attentional processing hosted by this crucial node of the frontoparietal attention network.

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