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Hemispheric Asymmetries in Visuospatial Attention: Functional Dissociations and Modulation of Visual Processing

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Declaration of Authorship

I hereby declare that the contents and organization of this dissertation constitute original work and do not compromise in any way the rights of third parties, including those relating to the security of personal data.

17 December 2025

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To my grandparents, Dario and Luigina

Summary

Publications: Preprints and Journal Articles

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- ***Tosi, M.****, Ellena, G., Contò, F., Edwards, G., & Battelli, L. (2026). Hemispheric Dissociation Revealed by Attentional Isolation and Transcranial Random Noise Stimulation. Journal of Cognitive Neuroscience, 1–11. Advance online publication. https://doi.org/10.1162/JOCN.a.2587*
- *Contò, F.*,* ***Tosi, M.*****, Ellena, G., Cattaneo, Z., & Battelli, L. - From networks to cognition: Integrating brain stimulation and neuroimaging to study visuo-attentional functions [Manuscript in preparation]. *Authors contributed equally to this work*
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- *Contò, F., Ellena, G., Edwards, G.,* ***Tosi, M.****, & Battelli, L. (2026). Brain stimulation prevents neural downregulation and optimizes learning. NeuroImage, 329, 121824. https://doi.org/10.1016/j.neuroimage.2026.121824*
- *Conto, F., Ellena, G.,* ***Tosi, M.****, Peatfield, N. A., & Battelli, L. (2025). The effect of rTMS on neural correlates of time perception. Transcranial Magnetic Stimulation, 5, 100187. https://doi.org/10.1016/j.transm.2025.100187*

List of Abbreviations

2AFC	Two-alternative forced choice
AG	Angular Gyrus
AIPS	Anterior Interparietal Sulcus
ALFF	Amplitude of Low-Frequency Fluctuation
ANT	Attention Network Test
APA	American Psychological Association
BOLD	Blood Oxygenation Level Dependent
BP-tCAS	Bilateral Parietal Alternating Current Stimulation
CI	Confidence Interval
CP	Critical Period
cTBS	Continuous Theta Burst Stimulation
DAN	Dorsal Attention Network
DLPFC	Dorsolateral Prefrontal Cortex
DVAN	Dorso Ventral Attention Network
E/I	Excitation/Inhibition
EEG	Electroencephalography
EMMs	Estimated Marginal Means
ERP	Event Related Potential
FA	Fractional Anisotropy
FC	Functional Connectivity
FEF	Frontal Eye Fields
FINST	Fingers of Instantiation
fMRI	Functional Magnetic Resonance Imaging
FOOOF	Fitting Oscillations and One-Over-f
FP	Frontoparietal
GABA	γ-Aminobutyric Acid
GLMM/glmer	Generalized Linear Mixed-Effects Model
HF	High Frequency
HMOA	Hindrance Modulated Orientational Anisotropy
hMT	Human Middle Temporal
IAF	Individual Alpha Frequency
ICF	Intracortical Facilitation
ICI	Intracortical Inhibition
IFG	Inferior Frontal Gyrus
IFOF	Inferior Fronto-Occipital Fasciculus
IGI	Intracortical GABAergic Inhibition
IPC	Intraparietal cortex
IPL	Inferior Parietal Lobule
IPS	Intraparietal Sulcus
ISI	Interstimulus Interval

iTBS	Intermittent Theta Burst Stimulation
ITG	Inferior Temporal Gyrus
lmer	Linear Mixed-Effects Model
LPS	Lateral Peristriate Cortex
lSPL	Left Superior Parietal Lobule
LTD	Long-term Depression
LTP	Long-Term Potentiation
M1	Primary Motor Cortex
MEG	Magnetoencephalography
MFG	Middle Frontal Gyrus
MOG	Middle Occipital Gyrus
MOT	Multiple Object Tracking
mPFC	Medial Prefrontal Cortex
MRI	Magnetic Resonance Imaging
MRS	Magnetic Resonance Spectroscopy
mSPL	Medial Superior Parietal Lobule
MST	Middle Superior Temporal
MT	Middle Temporal
MT+	Middle Temporal Complex
NIBS	Non-Invasive Brain Stimulation
NMDA	N-methyl-D-aspartate
OWM	Non-Spatial Object Working Memory
PIPS	Posterior Interparietal Sulcus
PMv	Ventral Premotor Cortex
PPC	Posterior Parietal Cortex
PrCe	Precentral Cortex
PV	Parvalbumin Interneurons
ReHo	Regional Homogeneity
rIPL	Right Inferior Parietal Lobule
RSFC	Resting State Functional Connectivity
rTMS	Repetitive Transcranial Magnetic Stimulation
RVIP	Rapid Visual Information Processing
SD	Standard Deviation
SLF	Superior Longitudinal Fasciculus
SMA	Supplementary Motor Area
SMG	Supramarginal Gyrus
SPL	Superior Parietal Lobule
SR	Stochastic Resonance
SST	Somatostatin Interneurons
SSVEPs	Steady State Visual Evoked Potentials
STDP	Spike-Timing-Dependent Plasticity
STG	Superior Temporal Gyrus
SWM	Spatial Working Memory
tACS	Transcranial Alternating Current Stimulation
TBS	Theta Burst Stimulation

tDCS	Transcranial Direct Current Stimulation
tES	Transcranial Electrical Stimulation
TMS	Transcranial Magnetic Stimulation
TOS	Transverse Occipital Sulcus
TPJ	Temporoparietal Junction
tRNS	Transcranial Random Noise Stimulation
V1	Visual Area 1
V2	Visual Area 2
V3	Visual Area 3
V3a	Visual Area 3A
V4	Visual Area 4
V5	Visual Area 5
VAN	Ventral Attention Network
VFC	Ventral Frontal Cortex
vIPS	Ventral Intraparietal Sulcus
VIT	Visual Indexing Theory
VRLAT	Virtual Reality Lateralized Attention Test
VSTM	Visual Short-Term Memory

Thesis abstract

Visuospatial attention is one of the most studied psychological constructs. It represents a central mechanism for regulating human cognition, facilitating the selection and integration of stimuli from the surrounding world. To date, the study of visuospatial attention has relied on traditional methods, such as behavioral data and techniques for measuring brain function, including neuroimaging and neurostimulation. Recently, a growing body of literature has focused on how specific procedures can enhance cognitive and attentional performance, while also investigating the neural bases underlying these effects.

After providing a theoretical overview that defines the framework for studies on visuospatial attention (Chapter 1), we reviewed the current methodologies for investigating this construct through a systematic approach (Chapter 2), with particular emphasis on the integration of Non-invasive Brain Stimulation (NIBS) with multimodal neuroimaging, highlighting both the strengths and limitations of the current state of the art.

Building on this foundation, we investigated the neural mechanisms of plasticity induced by prolonged spatial attentional imbalance. We examined how this imbalance, combined with NIBS, can be used to clarify the respective roles of the right and left hemispheres in supporting visuospatial attention (Chapter 3). In particular, attentional imbalance and the resulting enhancement in visual attention performance appear to be induced and modulated by plasticity-dependent mechanisms, which are central to the theoretical framework of interhemispheric competition.

Finally, the neural and electrophysiological bases underlying attentional imbalance and the associated enhancement in visual attention performance were preliminarily investigated using electroencephalography (EEG) - (Chapter 4). The thesis concludes with final remarks and future directions (Chapter 5).

General introduction

Our world is characterized by continuous sensory stimulation, originating both from external and internal sources. To function effectively, individuals must respond to this information adaptively and selectively. For example, in a social context, maintaining a conversation requires focusing on a conversational partner while filtering out irrelevant sounds and other competing stimuli. The same is true when watching a movie or taking notes during a lesson. The human brain, therefore, acts dynamically, focusing, filtering, and redirecting attention based on the context (Desimone & Duncan, 1995; Driver, 2001; Petrucci & Pecchinenda, 2017). These mechanisms are typically studied using neuropsychological experimental paradigms to examine their neural and cognitive bases (Carrasco, 2011; Fernández & Carrasco, 2020; Mirsky, 2018). Attention is a key construct in cognitive psychology and cognitive neuroscience, widely studied in neurotypical subjects and patients (Giglhuber et al., 2017; Turatto et al., 2000; Umiltá, 1995). The tools used today mainly include paper-and-pencil tests (Bonato et al., 2012), interactive computer tasks (Bonato et al., 2013; Van Heugten et al., 2022), neurophysiological measures (EEG, MEG) – (Taylor & Thut, 2012; T. W. Wilson et al., 2018), and functional/structural measurements (fMRI, MRI) – (Battelli et al., 2017; Mitko et al., 2019; Schintu et al., 2021). These tools have enabled a shift from the paradigm of clinical observation of individual subjects to more standardized studies with homogeneous measurement methods. Building upon this, several systematic reviews and meta-analyses have highlighted the importance of neuroenhancement and neurorehabilitation methods for patients with brain injury (Lawrence et al., 2017; Montana et al., 2019; Saa et al., 2021). These approaches include rehabilitation and cognitive enhancement strategies based on specific behavioral procedures and exercises, as well as NIBS techniques that modulate neural plasticity and homeostatic balance mechanisms that support cognitive processing. For instance, NIBS shows potential benefits for attention, working memory (WM), and executive function recovery in stroke patients, as well as for global cognition (Hara et al., 2021). Indeed, NIBS has been widely used to modulate attentional reorienting (Ciavarro et al., 2013; Lojowska et al., 2025; Sengupta et al., 2024), sustained attention (Edwards et al., 2020; Nelson et al., 2014; Richard et al., 2018; van Schouwenburg et al., 2021), and covert/overt attention (Bien et al., 2012; Cazzoli et al., 2015; Gurel et al., 2018), making it a crucial tool for patients with cognitive deficits (Zebhauser et al., 2019).

Studies on interhemispheric differences in attentional processing have demonstrated that a loss of interhemispheric balance following unilateral cortical damage can cause severe, long-term disruption of attentional functions (Duecker & Sack, 2015; Vallar et al., 2014; Veronelli & Vallar, 2025). These disruptions may result from anatomical and functional constraints. In particular, it is well known that the left and right hemispheres may have different roles in supporting attention (Heilman et al., 2000; Heilman & Valenstein, 1979; Heilman & Van Den Abell, 1980). These differences, known as "asymmetries," have been extensively studied from behavioral, anatomical, and neurophysiological perspectives (Zebhauser et al., 2019). Although correlational functional studies have demonstrated the presence of these asymmetries when tested using classical attentional paradigms (Corbetta & Shulman, 2002, 2011) they failed to reveal causation between the brain and behavior. NIBS tools are essential for studying the dissociations and differences between the two hemispheres (Duecker & Sack, 2015; Giglia et al., 2011; Plow et al., 2014). This thesis focuses on visual and spatial attention and, in the experimental chapters, examines how a targeted attentional manipulation—where participants sustain attention within a single visual hemifield while actively suppressing the contralateral hemifield—can be used to probe hemispheric asymmetries and modulate behavioral responses through non-invasive brain stimulation.

The theoretical definition of visuospatial attention as a construct is complex and remains the subject of ongoing debate, as it reflects a non-unitary phenomenon (Hommel et al., 2019; Scholl, 2009; W. Wu, 2023). Historically, attention has been conceptualized as the brain's ability, within a cognitive framework, to concentrate and direct awareness toward specific stimuli while excluding others (James, 1890; Laberge, 1990). The term attention is therefore best understood as an umbrella construct encompassing multiple concepts, including selective attention (filtering out irrelevant stimuli while prioritizing others) - (Broadbent, 1958), divided attention (sharing attentional resources across simultaneous tasks) - (Kahneman, 1973), orienting (shifting and maintaining attentional focus) – (Posner et al., 1980) and visuospatial attention (processing information based on the spatial location of stimuli) - (Posner et al., 1980; Rizzolatti et al., 1987; Treisman & Gelade, 1980). Given the broad and multifaceted nature of the attention construct, this thesis will primarily focus on visuospatial attention, as defined by Desimone and Duncan (1995) - (see *Chapter 1, Section 1.1*).

The theoretical construct of visuospatial attention relies on large-scale brain networks (such as the dorsal and ventral attention networks - DVAN) - (Contò et al., 2021) - and partly overlaps with other psychological domains, including WM and executive functions (Baddeley, 1992, 2000; Repovš & Baddeley, 2006; Zhou et al., 2021). A substantial portion of this manuscript is dedicated to the concept of interhemispheric interaction and to how such interactions may influence and modulate visuospatial attention. The notion of interhemispheric asymmetry is grounded in neuropsychological evidence from patients with unilateral brain damage, particularly right-hemisphere lesions associated with hemineglect, which have been instrumental in revealing asymmetric contributions of the two hemispheres to attentional control (Vallar, 2001; Vallar & Calzolari, 2018; Vallar & Perani, 1986; Veronelli & Vallar, 2025). Hemispatial neglect is a heterogeneous syndrome characterized primarily by visuo-attentional deficits, resulting in a loss of awareness of the hemifield contralateral to the lesion (Corbetta, 2014; Koch et al., 2013; Moore et al., 2023). The right hemisphere is generally dominant for spatial representation, primarily by controlling the direction and strength of the attentional gradient (Bisiach et al., 1986; Kinsbourne, 1987; Mesulam, 1981; Veronelli & Vallar, 2025). The concept of an attentional gradient, originally proposed by Kinsbourne and subsequently elaborated by other authors, posits the existence of a spatially distributed bias in attention across the horizontal dimension of space. Within this neuropsychological framework, the gradient is thought to arise from an interhemispheric imbalance, ultimately influencing the representation and conscious awareness of visual space (Sacher et al., 2004).

The dynamic balance between excitation and inhibition constitutes a core mechanism underlying visuospatial attention. In particular, the brain maintains a homeostatic balance between the two hemispheres, an essential process for the regulation and stability of visuo-attentional functions (Brighina et al., 2003; Koch et al., 2004). Transcallosal pathways likely manage the balance of excitation and inhibition between the hemispheres. If this balance is lost, the brain's natural equilibrium (homeostasis) is disrupted (Giglhuber et al., 2017; Nyffeler et al., 2008; Schintu et al., 2021). For example, applying inhibitory stimulation to the right PPC reshapes connectivity within the attentional network, though this effect depends on existing interhemispheric connectivity (Schintu et al., 2021; Battelli et al., 2009). Finally, the resulting cerebral asymmetry in brain activation following a cerebrovascular event is hypothesized to be responsible for the symptomatology due to excessive inhibition from the healthy to the affected parietal attention regions (Brancaccio et al., 2022).

The severity of symptomatology is also related to this difference in brain activation (Harquel et al., 2024; Lasaponara et al., 2019; Pirondini et al., 2020). Some seminal studies have shown that interhemispheric competition can occur between homologous areas in the two hemispheres, ranging from sensory to motor areas (Carson, 2020; Ferbert et al., 1992; Koch et al., 2008; Petitet et al., 2015). For example, prolonged visual sensory deprivation or unilateral motor training can paradoxically increase performance in healthy participants, as evidenced by shifts in ocular dominance, changes in visual evoked potentials (VEPs), and increased motor performance (Andrushko et al., 2023; Lim & Madhavan, 2023; Lunghi, Berchicci, et al., 2015). Studies on monocular deprivation, in particular, have provided evidence that prolonged deprivation can result in a shift in ocular dominance toward the deprived eye (Steinwurzel et al., 2025). These effects show potential for use in neurorehabilitation if transfer to the attentional and visual domains can be achieved. Together, these studies suggest that when homologous areas in the two hemispheres compete during a task, it can lead to paradoxical facilitation. Multiple behavioral tasks have been developed over the years to assess the efficacy of neurorehabilitation interventions, particularly in the domain of visuospatial attention. Among these, the Multiple Object Tracking (MOT) task is a computerized paradigm that has proven highly efficient for measuring sustained visuospatial attention (Howe et al., 2009; H. Li et al., 2023). The rationale for using the MOT paradigm can be clarified by emphasizing its suitability for investigating sustained attention in situations that resemble real-world demands. Unlike many traditional laboratory tasks, which isolate attention at a single spatial location or over brief intervals, MOT requires participants to continuously monitor multiple moving targets distributed across both visual hemifields over extended periods of time. This simultaneous, dynamic allocation of attentional resources places sustained demands on attentional capacity and control. Thus, MOT more accurately captures the spatiotemporal complexity of everyday visual environments, in which attention must flexibly shift across multiple objects and locations. For these reasons, the MOT paradigm is a particularly appropriate and ecologically valid framework for investigating sustained attention (Minami et al., 2019). During bilateral tracking, the allocation of attentional resources to the two hemifields can be manipulated in a way similar in principle to the monocular deprivation paradigm. This has been done in a recent study by our group, showing that prolonged imbalance of attention in a single visual hemifield is essential for achieving a paradoxical increase in attentional performance in the contralateral hemifield (Edwards et al., 2021).

This thesis tests the increase in performance detected through attentional isolation using tRNS. It investigates the role of the right and left hemispheres within the framework of interhemispheric competition and analyzes the possible homeostatic plasticity mechanisms involved. Specifically, tRNS was applied over key nodes of the Dorsal Visual Attention Network (DVAN) as identified in prior fMRI studies (Battelli et al., 2017; Contò et al., 2021; Culham et al., 1998). The Frontal Eye Fields (FEF) and Intraparietal Sulcus (IPS) are critically involved in sustained attention and Multiple Object Tracking (MOT), making them promising targets for this research. We stimulated the left and right FEF and IPS unilaterally on consecutive sessions; right-hemisphere sites corresponded to F2 and P4, while left-hemisphere sites corresponded to F1 and P3 in the international 10-20 EEG system. These coordinates were selected as functional proxies due to the absence of neuronavigation and the relatively large surface area of the electrodes.

Finally, the neural correlates of attentional isolation were also analyzed, with preliminary results showing a significant change in components that are typically involved in visuoattentive processing.

1. CHAPTER 1: Visuospatial Attention: definition and experimental foundations

1.1. Theoretical Framework

1.1.1. Cognitive and neural foundations

Humans rely on dynamic tracking of visual stimuli, object recognition, and real-time updating of information during interaction with the external environment in their everyday lives. These skills are typically involved in many daily activities; for example, driving requires them. While driving, individuals must continuously process a vast amount of dynamic perceptual information, distinguishing what is relevant from what is not. It may also become necessary to rapidly shift attention to unexpected events, such as a pedestrian crossing the road, or to monitor the execution of actions like overtaking another vehicle. This typical everyday action requires the cooperation of different cognitive mechanisms to be executed successfully. The computational resources of the human brain are limited, so it is crucial to limit the processing of the external environment. To prevent information-processing overload, we must prioritize relevant information and ignore irrelevant information. This filtering must be sustained over time, given the moment-to-moment changes in the visual environment. Depending on the demands of the task, we must focus or diffuse our attention across the entire visual field, and this ability is what allows us to distinguish relevant stimuli from irrelevant ones.

Attention is formally defined by the American Psychological Association (APA) as "*a state in which cognitive resources are focused on certain aspects of the environment rather than others, and the central nervous system is ready to respond to stimuli*". This definition emphasizes the multisensory origins of the construct, spanning multiple cognitive domains. In the specific example we reported above, however, the emphasis is placed on the visual and spatial domains, thus defining the construct of visuospatial attention (Fu et al., 2010; Lochner & Trick, 2014). Visuospatial attention is the cognitive process that selectively modulates visual information processing according to spatial location, enhancing perception of relevant stimuli while suppressing irrelevant ones (Desimone & Duncan, 1995). This filtering mechanism optimizes limited neural resources and is supported by a distributed network of cortical and subcortical regions, primarily in the parietal and frontal cortices (Kastner & Ungerleider, 2000; Petersen & Posner, 2012; Posner & Petersen, 1990).

Visuospatial attention is closely linked to skills such as directing attention to different points in the visual field and focusing on the position, size, and orientation of visual stimuli. One of the most widely described models in the literature, which introduces the neural model of vision, is the two-stream hypothesis. This subdivision was first done in monkey studies and was further translated to humans while merging anatomical, neurological, neuropsychological, electrophysiological, and behavioral evidence for building the models (Baker & Kravitz, 2024; Kastner & Ungerleider, 2000; Mishkin et al., 1983; Ungerleider & Haxby, 1994). The two-stream hypothesis represents a foundational framework in neuropsychology, proposing that visual information is processed through two functionally and anatomically distinct cortical networks: the ventral ("what") stream and the dorsal ("where") stream (Goodale, 1994; Goodale & Milner, 1992). The ventral pathway, running from the primary visual cortex to the inferior temporal gyrus, specializes in color, space perception, high-level object recognition, and form representation. Meanwhile, the dorsal pathway, extending into the parietal areas, is crucial for spatial localization, motion detection, and guiding actions. Together, these two systems allow the brain to identify environmental stimuli and coordinate visuospatial attention for real-time interaction with the environment.

The ventral stream follows the occipitotemporal pathway and directly involves areas V1, V2, V3, and V4, which converge onto the inferior temporal gyrus (ITG). The dorsal pathway starts from the primary visual cortex, V1, V2, and V3, and continues upward toward the middle temporal (MT) and middle superior temporal (MST) areas, including the parietal areas. While imaging, neurophysiological, and neurological studies indicate that the ventral and dorsal streams are separate (Goodale, 1994; Pisella et al., 2009), other studies suggest that they converge and are interconnected

(Takahashi, 2013; Zanon et al., 2010). The study of visuospatial attention gained prominence in the 1980s with the introduction of the Posner cueing paradigm, which formalized the distinction between endogenous and exogenous attentional orienting. This experimental task provides a model of visual-attentive processing by examining the distribution of attention in response to external stimuli. The observer is asked to stare at the center while peripheral cues are presented. These cues may represent the exact appearance of the target (a valid trial) or an inaccurate position (an invalid trial) - Figures 1A and 1B. Reaction times are measured and vary depending on whether it is a valid trial (shorter) or an invalid trial (longer). Covert attention allows for the prioritization of stimuli without requiring eye or head movements. However, overt orienting, or foveating a stimulus, has also been shown to enhance visual target processing, particularly in terms of accuracy and detection (Cazzoli, Wurtz, et al., 2009; H. H. Li et al., 2021; Petersen & Posner, 2012; Posner & Petersen, 1990). Over the years, Posner's paradigm has been widely used to study the deployment and orientation of attention (Posner & Petersen, 1990).

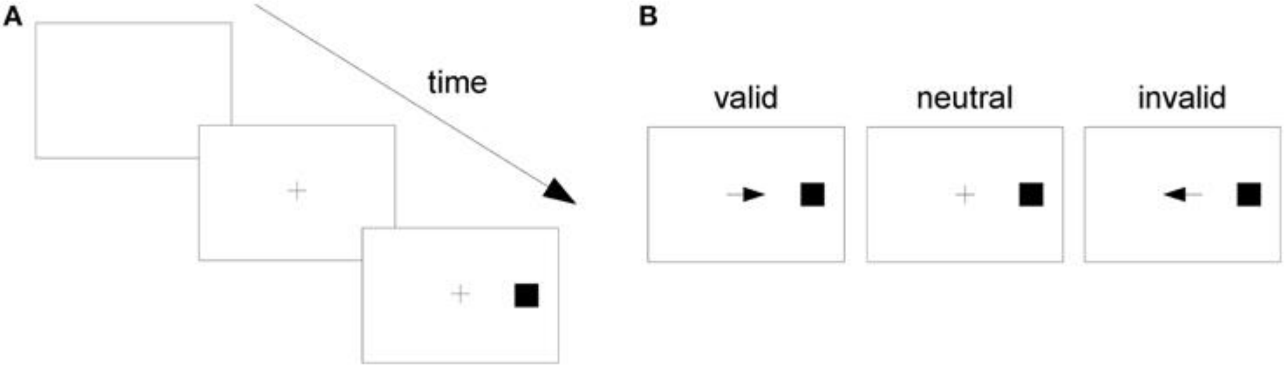

Figure 1 *- Typical Posner spatial cueing paradigm (adapted from Feher da Silva & Baldo, 2015).*

Physiologically, the Posner task has been associated with specific Event Related Potential (ERP) amplitude changes under valid cue conditions (Figure 2), and with multiple ERPs components (such as C1, P1, N1, and N2pc) - (Pan et al., 2024; Qin et al., 2022, 2023; Slotnick, 2018). Specifically, greater attentional focus, facilitated by valid cues in the Posner task, is associated with significant changes in P1 and N1 amplitudes, reflecting an efficient “attentional priming” effect of early sensory processing compared to the control conditions (X. Liu & Sun, 2017; Perchet et al., 2001). Transitioning from the early sensory to a higher cognitive level, the N2-posterior-contralateral (N2pc) response has been extensively studied in Posner-like paradigms. Specifically, this component reflects selective attention mechanisms, with brain activity primarily localized over the contralateral visual cortex in relation to the attended location in space. It has previously been linked to spatial selection and attention shifts (Kiss et al., 2008; Luck & Hillyard, 1994).

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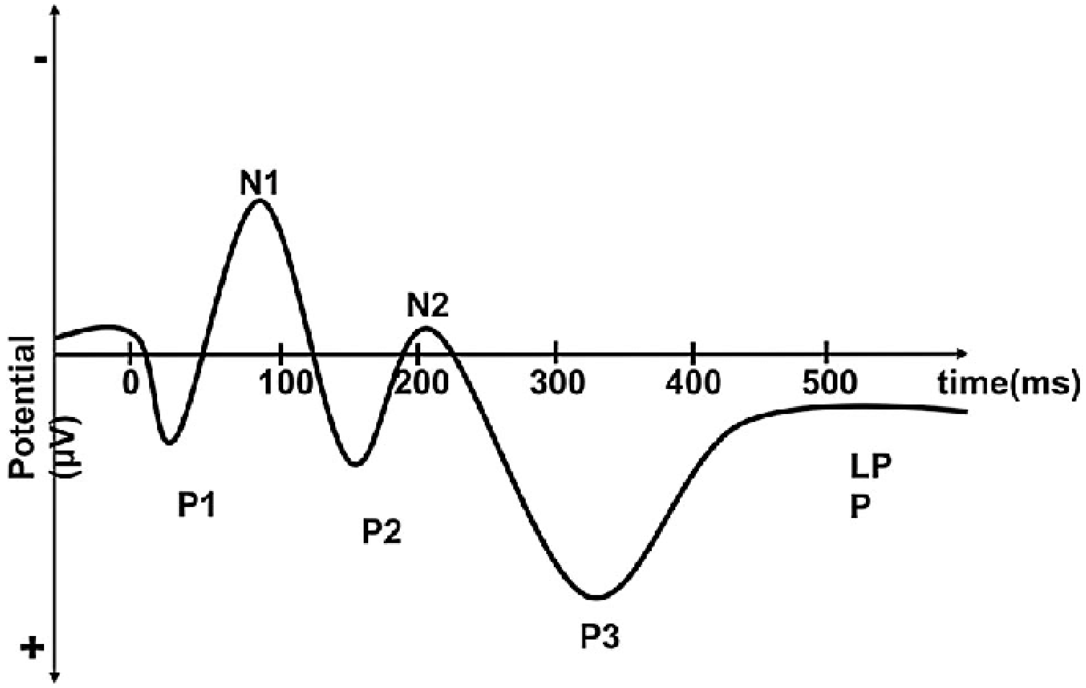


Figure 2 *- Image adapted from Eisenbarth, H. (2018). This image illustrates the main components of an ERP signal, highlighting changes in amplitude over time. Each component is associated with specific latencies, time windows, and peaks.*

Neuroimaging evidence has revealed the Temporoparietal Junction's (TPJ) role in Posner-like paradigms when comparing invalid and valid target stimuli, especially when attention must shift to an unexpected location. Neural evidence also suggests an asymmetry in TPJ activation, with the right hemisphere being preferentially recruited (Vossel et al., 2009). Prominent activation of the intraparietal cortex (IPC), as well as the Supramarginal Gyrus (SMG) and the Angular Gyrus (AG), has been associated with a role in endogenous orienting and, consequently, in top-down attentional expectations (Vossel et al., 2006). These findings underscore the modulatory influence of expectation on attentional allocation and subsequent brain activation (Doricchi et al., 2010).

1.1.2. Multiple Object Tracking (MOT) as a Paradigm for Studying Attention

For many years, the study of visuospatial attention has been confined to experimental paradigms applicable only in a laboratory setting. One of the main limitations of this field is the difficulty of generalizing these results to a real-world context (Marion et al., 2025). Indeed, the neuropsychological framework is shifting towards a major emphasis on clarifying the relationship between task performance and everyday life, thus revealing possible limitations in the assessment of neuropsychological batteries and tests (Chaytor et al., 2006; Frederick & Bowden, 2009; Gioia & Isquith, 2004; Spooner & Pachana, 2006). One of the most useful skills in real-life scenarios is the ability to analyze information from the external environment, even simultaneously. One of the tasks that most closely resembles the characteristics of the external world is MOT, developed in the late 1980s by Pylyshyn and Storm (1988). Emerging evidence supports a partial generalization of the cognitive mechanisms (especially visuospatial attention) engaged during MOT in complex real-world scenarios (Michaels et al., 2022, 2023). This task is primarily a visual search task, with some target/distractor stimuli presented on the screen in the right and left hemifields. Through an initial blinking event, a subset of these dots is signaled as the target subset. During a movement phase, where all the targets and distractors are moving in random trajectories, the participant's task is to discriminate the target dots from the distractor dots. Tracking performance is defined as the participant's ability to distinguish target stimuli from distractor stimuli (Figure 3). MOT has specific characteristics that distinguish it from normal visual and attentional tasks. As Scholl (2001) showed, MOT requires the ability to sustain attention on stimuli over time. MOT also involves distributing attention across multiple objects simultaneously. According to Scholl's (2009) review, MOT is characterized by a pre-attentive indexing component that acts as a bridge between the external world, visual perception, and cognition. Specifically, indexing refers to the brain's ability to identify and retain information about objects of interest (Z. W. Pylyshyn, 2001). However, various studies show that the attentional component of sustained tracking is also described by electrophysiological variations in later attentional processes. Therefore, it is implicit that there is a relationship between tracking, fatigue, and cognitive modulation that extends beyond preallocation and attentional indexing (Guo et al., 2016; Scholl, 2001, 2009)

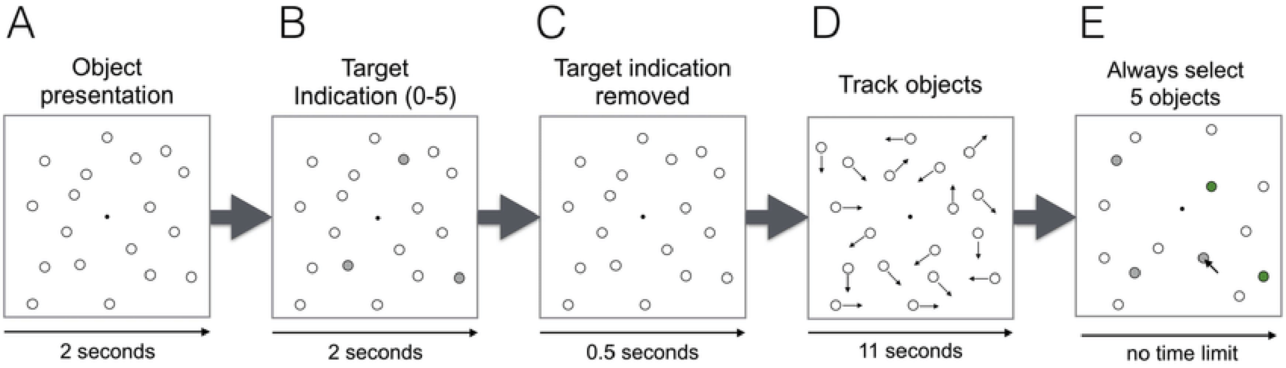


Figure 3 - Typical Multiple Object Tracking task stimuli presentation and detection - *In the first frame (A), objects are presented and subsequently indicated as targets (B). In (C), target indications are removed, and the objects start to move (D) for a predefined time window. Finally, participants are prompted to detect the target among distractors (E) – modified from Wahn et al., 2016.*

Over the years, MOT has been widely used to study important aspects of attention, such as sustained, selective, and divided attention. A central contribution of this paradigm is its ability to distinguish whether attentional tracking operates within a retinotopic coordinate system based on retinal activation or an allocentric coordinate system based on global spatial coordinates (Amano et al., 2009; Dumoulin & Wandell, 2008; Huk et al., 2002; Wandell et al., 2007; Wandell & Winawer, 2011). Physiological studies have demonstrated how neurons in the early visual cortex maintain the spatial relationship of visual stimuli across the visual field (D. W. Bressler & Silver, 2010; Tootell et al., 1998) and how active tracking is not strictly bound to retinotopic mapping (Meyerhoff et al., 2017). In different experimental conditions, visual tracking performance has been shown to depend on contextual and multiple cognitive factors (H. Li et al., 2023). In particular, the literature highlights the roles of online processing capacity and higher-order cognitive functions, such as WM. Various studies have also examined the role of WM in attentive tracking (Heuer et al., 2016; Xuan et al., 2010). Typically, the WM span ranges from four to eight in neurotypical subjects (Luck & Vogel, 1997; Miller, 1956). Within the typical tracking framework of MOT and related cognitive load, WM span is around five or six elements (Z. Pylyshyn, 1989; Z. W. Pylyshyn, 2001; Z. W. Pylyshyn & Storm, 1988). Extensive research demonstrates a significant correlation between WM and MOT. Evidence suggests that MOT training may yield a partial transfer of benefits to WM span. (Vartanian et al., 2016). Additionally, it has been shown that MOT may not rely entirely on early, purely pre-attentive processes, but instead also depends on the central executive component of WM, likely through the continuous comparison of successive target object files and the inhibition of new ones that could be triggered by the targets' moment-to-moment positional changes (Allen et al., 2006). Further evidence shows that MOT and WM are linked, indicating a decline in performance on both tasks in dual-task conditions (Lapierre et al., 2017; H. Li et al., 2023). The core finding of the study by Li et al. (2023) is that MOT relies specifically on spatial working memory (SWM) rather than Non-Spatial Object Working Memory (OWM). Through a series of dual-task experiments, the researchers observed that performing a concurrent nonspatial OWM task (like an auditory N-back task involving digits) did not significantly impair tracking capacity, indicating that these two processes are relatively independent. In contrast, a concurrent SWM task significantly reduced tracking performance, with the level of impairment increasing alongside the spatial memory load. These results challenge traditional "pure attention" models, such as those by Alvarez and Franconeri (2007), by demonstrating that MOT is not just an attentive process but one that actively consumes spatial working memory resources.

1.1.3. Hemifield-Based Experimental Paradigms: Unilateral and Bilateral Designs

Neuropsychological evidence in studies with neurological patients has been crucial in describing the relationship between visual and spatial attention and the concept of interhemispheric specialization

(Gazzaniga, 2000). Within the early visual system, input from the left visual field is projected to the right visual cortex, and input from the right visual field is projected to the left visual cortex. This division begins at the optic chiasm, where fibers from the nasal retinas cross to ensure that each hemisphere receives input from the opposite visual field. These signals are then organized within the lateral geniculate nucleus of the thalamus before reaching the cortex. This structural separation is maintained in the early stages of visual processing, specifically in the early visual areas (V1–V5), where receptive fields are small and respond to contralateral visual input (Huberman et al., 2008; Wandell et al., 2007). However, as information proceeds along the visual pathways (in high-order integration areas), inputs from the two hemifields tend to be integrated, neural receptive fields are wider and overlap (Ungerleider & Haxby, 1994).

Dynamic attentional tracking, which is typically exerted in MOT and similar tasks, has been shown to be constrained by independent attentional resources in the left and right hemifields (Alvarez & Cavanagh, 2005). Alvarez and Cavanagh showed that participants could track approximately twice as many targets when they were distributed across both hemifields as when they were confined to one. This bilateral advantage in visual tracking may reflect a general mechanism that reduces the cost of distributing attentional resources across hemifields (Malinowski et al., 2007; Müller et al., 2003). Similar hemifield segregation principles have also been observed in visual crowding, where external interference, competition, and integration processes occur (Chakravarthi & Cavanagh, 2009). Following Malinowski and colleagues' studies (2007), the debate has focused on the attentional spotlight and the possibility of modulating visual and spatial attention within one visual hemifield. However, these results did not explain how attention could be directed to multiple positions within a hemifield. Malinowski et al. (2007) showed that the attentional spotlight could be divided into separate foci, even when both targets are within the same hemifield. However, overall performance is lower compared to bilateral presentations. Steady State Visual Evoked Potentials - SSVEP - results partially supported the behavioral findings by showing amplitude changes reflecting the subdivision of attention, but only under specific spatial conditions (Malinowski et al., 2007). The spatial distribution of objects across hemifields has also been shown to improve VSTM. Specifically, VSTM for spatial locations improves when stimuli are distributed between the two visual fields. This might suggest some degree of hemifield independence in storage capacity (Delvenne, 2005).

For example, in a change detection task, participants were briefly presented with small white squares within predefined frames. After a brief retention period, either an identical display or a display with one shifted square appeared. Participants judged whether the two displays matched. Importantly, performance was higher when the squares were distributed across opposite hemifields (between conditions) than when they were confined within the same hemifield (within condition). These results suggest that VSTM for spatial locations is enhanced by bilateral stimulus distribution. This finding is consistent with the hypothesis that attentional and mnemonic resources function independently in the left and right visual fields (Delvenne, 2005). Further evidence from ERP markers of memory processing suggests that better performance in bilateral conditions likely reflects more efficient resource allocation and enhanced spatial selectivity. Nevertheless, the overall capacity limit of VSTM remains at approximately three to four items (Delvenne et al., 2011).

1.1.4. Neural correlates of MOT

Multiple studies have investigated cortical and neurophysiological changes associated with active tracking in the MOT paradigm, focusing on Blood Oxygen Level-Dependent (BOLD) responses, functional connectivity, and electrophysiological dynamics. Traditionally, research on attentional deployment has relied on paradigms such as the Posner cueing task or visual search. These paradigms are well-suited to examining the operation of a unitary attentional spotlight. However, MOT provides a unique framework for studying attention because it requires the simultaneous engagement of multiple visuospatial and attentional mechanisms when stimuli are presented bilaterally or unilaterally. Unlike the passive monitoring of perceptual features, MOT requires an active system that continuously updates and verifies the correspondence between spatial tags (location-based attentional labels) and tracked objects over time. Functional and visual psychophysical studies indicate that MOT involves low-level perceptual and motion processing as well as higher-order control functions (Jovicich et al., 2001; Lochner & Trick, 2014; Z. W. Pylyshyn, 2001; Tran & Hoffman, 2016; Vogel & Luck, 2000). Several functional magnetic resonance imaging (fMRI) studies have been run to identify the neuroanatomical substrates of tracking. The goal is to discriminate brain activity specific to the active attentive tracking component of the task (Culham et al., 1998; Jovicich et al., 2001). The study by Culham and colleagues (1998) is particularly relevant for understanding how attention can be divided among multiple spatial locations at once. The strongest activation during the MOT task was found in the parietal areas: Intraparietal Sulcus (IPS) and the Transverse Occipital Sulcus (TOS). Strong activation was also identified in frontal areas, especially the Frontal Eye Field (FEF). Modest activation was also found in the Middle Temporal Complex (MT+) and V3a for attentive tracking. However, activation in these two areas appears weak and is mainly mediated by the sensory component of movement rather than the attentional component.

Similarly, early retinotopic areas (V1/V2/V3) were primarily activated by saccadic eye movements and were never reported as engaged during attentive tracking. Building on this, the results indicate that attentional modulation not only amplifies pre-existing low-level visual activity but also relies on the recruitment of additional parietal and frontal areas. Additionally, Jovicich et al. (2001) reported overlapping results, with the strongest activation observed in the parietal area during tracking, weaker activation in V5/ MT+, and no relevant activation in V1 (Figure 4).

Based on this, Howe et al. (2009) identified a significant distinction in fMRI activation related to MOT, distinguishing between the processes of tracking and discriminating targets. The authors found significant differences in the fMRI activation during the MOT task between tracking and target discrimination. The study explored three experimental conditions: “attended moving,” “attended stationary,” and “passive viewing”. Consistent activation was found in the FEF, Anterior Interparietal Sulcus (AIPS), Superior Parietal Lobule (SPL), Posterior Intraparietal Sulcus (PIPS), and the Human Middle Temporal (hMT+). The AIPS emerged as a key node within the tracking network. The AIPS is functionally connected with the PIPS, the SPL, and the FEF, and seems to play a central role in the online monitoring of tracking and coordination of these areas (Howe et al., 2009).

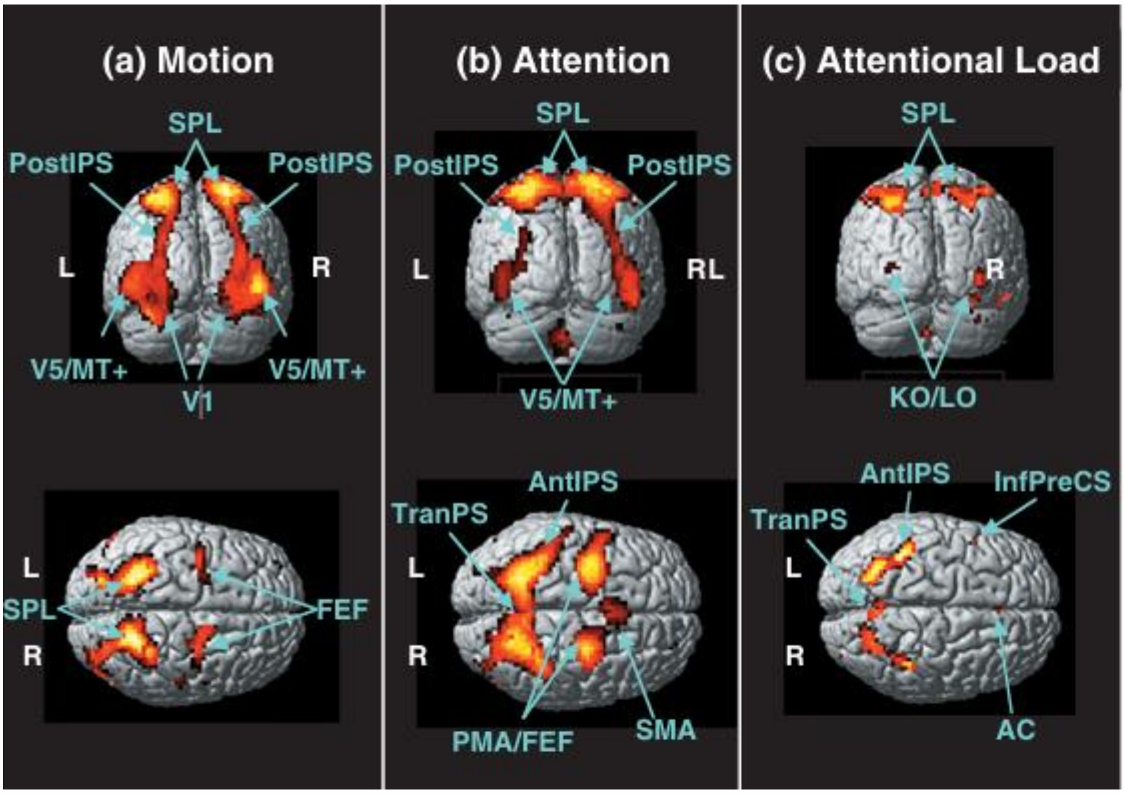


Figure 4 *– Averaged brain activation across subjects (*$p < .05$ *corrected for multiple comparisons) in different experimental conditions involving MOT tracking. This figure illustrates the average activation across subjects, differentiating between the motion (a, passive viewing of the moving balls compared to fixation) and tracking (b, active areas during active tracking of the moving balls compared to the passive condition). The attentional load condition (c) corresponds to the number of actively tracked targets, showing a linear increase in activation. Specifically, there is a positive relationship between the number of attended targets and the subsequent brain activation (Adapted from Jovicich et al., 2001).*

More recent data suggest that MOT-related activation may represent a promising tool for monitoring cognitive progress in clinical populations undergoing neurorehabilitation, thanks to its high test-retest reliability in network activation. Specifically, a greater cognitive improvement following training in stroke patients was associated with higher task-related BOLD activity during the MOT (Kolskår et al., 2020).

1.2. Interhemispheric Balance in Attention and Its Disruption

1.2.1. Hemispheric specialization in visuospatial functions

Another key point is that spatial attention is not distributed evenly across the visual field. Classic neuropsychological evidence of hemispheric asymmetries comes from patients with lesions in the right hemisphere, who often exhibit unilateral spatial neglect. This condition is characterized by severe impairments in allocating attention to the contralateral hemisphere (Bisiach et al., 1986; Heilman et al., 2000; Heilman & Valenstein, 1979; Mennemeier et al., 1997; Vallar & Perani, 1986; Veronelli & Vallar, 2025). These early patient studies provided strong support for the idea that the right hemisphere dominates attentional allocation (Aglioti et al., 1997; Bartolomeo & Chokron, 1999; Bartolomeo & Mandonnet, 2021; Esterman, 2000; Leibovitch et al., 1998, 1999; Lunven & Bartolomeo, 2017). Among these studies, Kinsbourne's interhemispheric competition theory proposed the idea that both hemispheres direct attention toward the contralateral visual field, exerting mutual inhibition to maintain healthy functioning (Kinsbourne, 1987). Importantly, the left-hemisphere attentional gradient toward the right visual field is somewhat stronger. Thus, when a lesion occurs in the right hemisphere, reducing its inhibitory influence over the left hemisphere, the left hemisphere becomes hyperactivated, which may lead to the manifestation of left hemineglect (Kinsbourne, 1987). Clinical observation on asymmetries in attentional deployment among the two hemispheres has also been further proven through noninvasive brain stimulation (Sparing et al., 2009).

Over the past decade, neuroimaging and neurophysiological approaches have extended this line of research and further characterized the neural bases of spatial neglect (Figure 5). These studies reveal the disruption of large-scale attentional networks in patients compared to healthy individuals, and they provide new insights into the functional reorganization of attentional circuits after brain damage (Baldassarre et al., 2014; Carter & Barrett, 2023; Pirondini et al., 2020; Spadone et al., 2022, 2023; Wiesen et al., 2022).

To understand how the mechanism for orienting visual attention compensates for disruption, it is useful to examine healthy individuals. There is evidence in the literature that neurologically healthy individuals exhibit a behavioral bias toward the left hemifield, a phenomenon known as pseudoneglect. This concept initially emerged from line bisection tasks and has since been supported by other similar paradigms (Cattaneo et al., 2009; Friedrich et al., 2018; Jewell & McCourt, 2000; Zago et al., 2017). This bias suggests an asymmetry in how the brain allocates attention across the visual field. Studies involving the Landmark and Line Bisection tasks have shown concurrent functional activation of the right IPS and the right LPS in healthy populations, which emphasizes the right hemisphere's prominent role in attentional allocation (Çiçek et al., 2009; Mennemeier et al., 1997; Schenkenberg et al., 1980; Zago et al., 2017). However, it is important to note that pseudoneglect can be affected by various factors, including handedness, eye dominance, the spatial location of stimuli, gaze direction, aging, and neurological disorders (Brignani et al., 2018; Friedrich et al., 2018; Learmonth & Papadatou-Pastou, 2022).

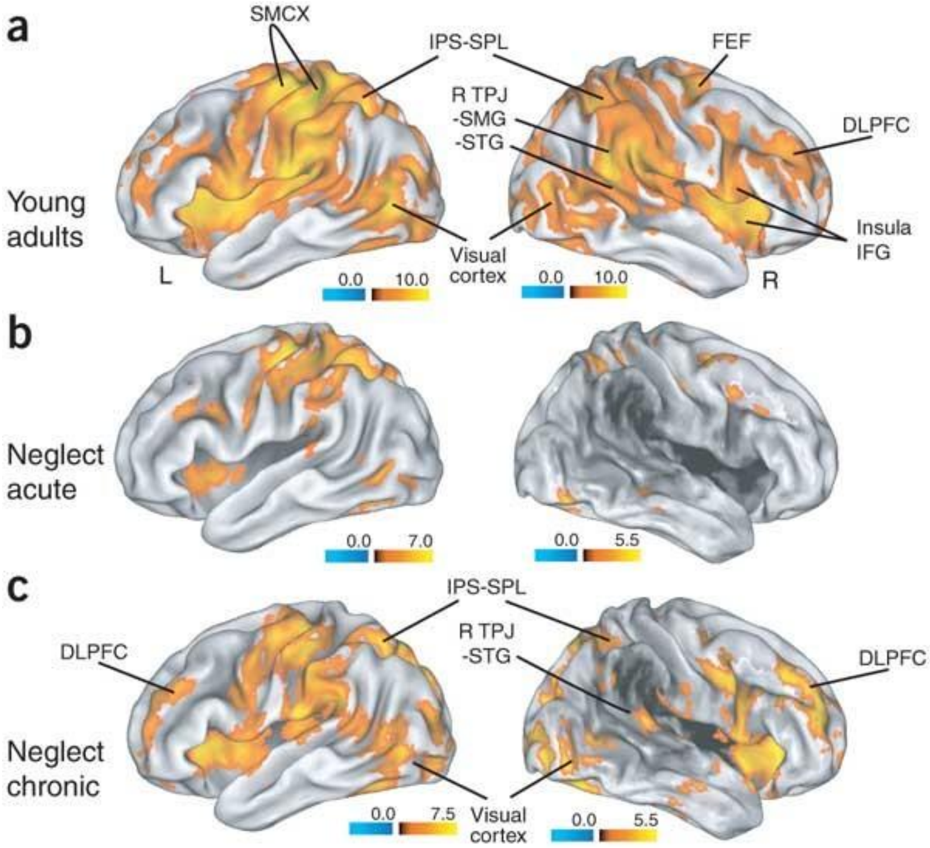


Figure 5 - *Brain activation patterns during the Posner task in neurotypical participants (a), acute neglect patients (b), and chronic neglect patients (c) reveal clear qualitative differences across clinical conditions. Neurotypical individuals showed widespread bilateral activation across occipital, parietal, temporal, and frontal cortices. In contrast, acute neglect patients exhibited weak or absent task-related activity in large portions of the right hemisphere, including occipital visual cortex, posterior parietal regions—particularly the IPS and* SPL *and DLPFC, despite these regions being structurally intact. At the chronic stage (39 weeks post-onset), partial recovery of right-hemisphere activity was observed, notably in the IFG, DLPFC, and STG, alongside additional changes in the left hemisphere, suggesting functional reorganization over time – Adapted from Corbetta et al., 2005.*

As discussed thus far, neurological and neuropsychological evidence from healthy subjects and patients indicates that visuospatial attention relies on mutual interhemispheric interaction between the two cerebral hemispheres. Another way to study this interaction in healthy participants has been used in a recent study conducted in our laboratory, where the authors manipulated interhemispheric balance using a procedure called "attentional isolation". Essentially, participants were asked to "isolate" their attention on one hemifield for an extended period of time. Following this isolation, benefits in gaze-contingent visual tracking were reported in the contralateral unattended hemifield (Edwards et al., 2021). This benefit was absent in a control bilateral-tracking condition. These results raise intriguing questions about the nature of interhemispheric interaction and its role in orienting attention.

1.2.2. Dynamic competition models of interhemispheric interaction

Typically, the human brain maintains a balance of excitation and inhibition across both cerebral hemispheres (Giglia et al., 2011; Nyffeler et al., 2009). Unilateral attentional deployment (in one hemifield) for a prolonged period of time in neurotypical subjects subsequently leads to behavioral improvement in visual-attentive performance in the contralateral, unattended hemifield (Edwards et al., 2021). One interesting question is about the physiological and molecular bases of the interhemispheric interaction, and one of the hypotheses is that the attentional enhancement observed following unilateral attentional deployment in the contralateral, unattended hemifield may be rooted in the homeostatic gain control mechanism (Muret & Makin, 2021) or post-inhibitory rebound spiking mechanisms of certain neural populations (Ferrante et al., 2017).

Other studies have further elucidated, from an electrophysiological perspective, how the two hemispheres communicate during visuospatial tasks. Recent literature has emphasized the critical role of alpha-band oscillations, revealing their spatial distribution and influence on spatial attention. Notably, suppression of alpha activity has been documented in the contralateral hemisphere following presentation of a visual stimulus in the opposite attended hemifield. Concurrently, the ipsilateral hemisphere of the attended hemifield displays heightened alpha band activity (Gomez-Ramirez et al., 2009; Kelly et al., 2006, 2009; Rihs et al., 2007). Typically, alpha-band suppression is associated with increased alertness and improved task performance. Similar findings were replicated in a magnetoencephalography (MEG) study (Ikkai et al., 2016). The primary aim of the study was to investigate the extent to which parieto-occipital alpha activity monitored the locus and spatial distribution of attention. Once again, desynchronization of alpha band power was observed, particularly in the contralateral hemisphere, in response to a validly cued visual target located in the opposite hemifield. This effect was particularly notable within the visual cortex. In contrast, when the visual target was not cued, desynchronization of the alpha band was distributed in a broad, non-specific manner over the parietal and occipital regions of both hemispheres. These results highlight the dynamic process of attentional orientation within the brain. This process might be specifically linked to the interdependent relationship between excitation and inhibition in the two cerebral hemispheres, which varies with alpha frequency.

Additional crucial direct evidence regarding the interplay between inhibition and excitation in visuospatial attention across the two hemispheres came from NIBS studies (see next section for a detailed explanation). Common features of these techniques include the ability to target and modulate specific brain areas and neural populations. The main hypothesis is that NIBS interfere with the mechanisms of excitation and inhibition (Herpich et al., 2018; Hordacre et al., 2017; Kortuem et al., 2019; Wittkopf et al., 2021) as well as the functional connectivity of large-scale brain networks (Battelli et al., 2017; Contò et al., 2021).

NIBS has been used to modulate hypothesized altered cortical excitability between the two hemispheres in patients with visuospatial neglect (F.A. Yang et al., 2023). For example, stroke neglect patients who received concurrent bilateral tDCS over the posterior parietal cortex (PPC) showed improvement in contralateral visuospatial deficits depending on the stimulation parameters and current polarity (see Figure 6 for an explanatory model). Improvement has been correlated with the upregulation of the affected, ipsilesional hemisphere and the downregulation of the contralesional healthy hemisphere (Sparing et al., 2009). Other studies have indicated that inhibitory repetitive Transcranial Magnetic Stimulation (rTMS) can also help patients with chronic post-stroke neglect recover their visuospatial functions (Agosta et al., 2014).

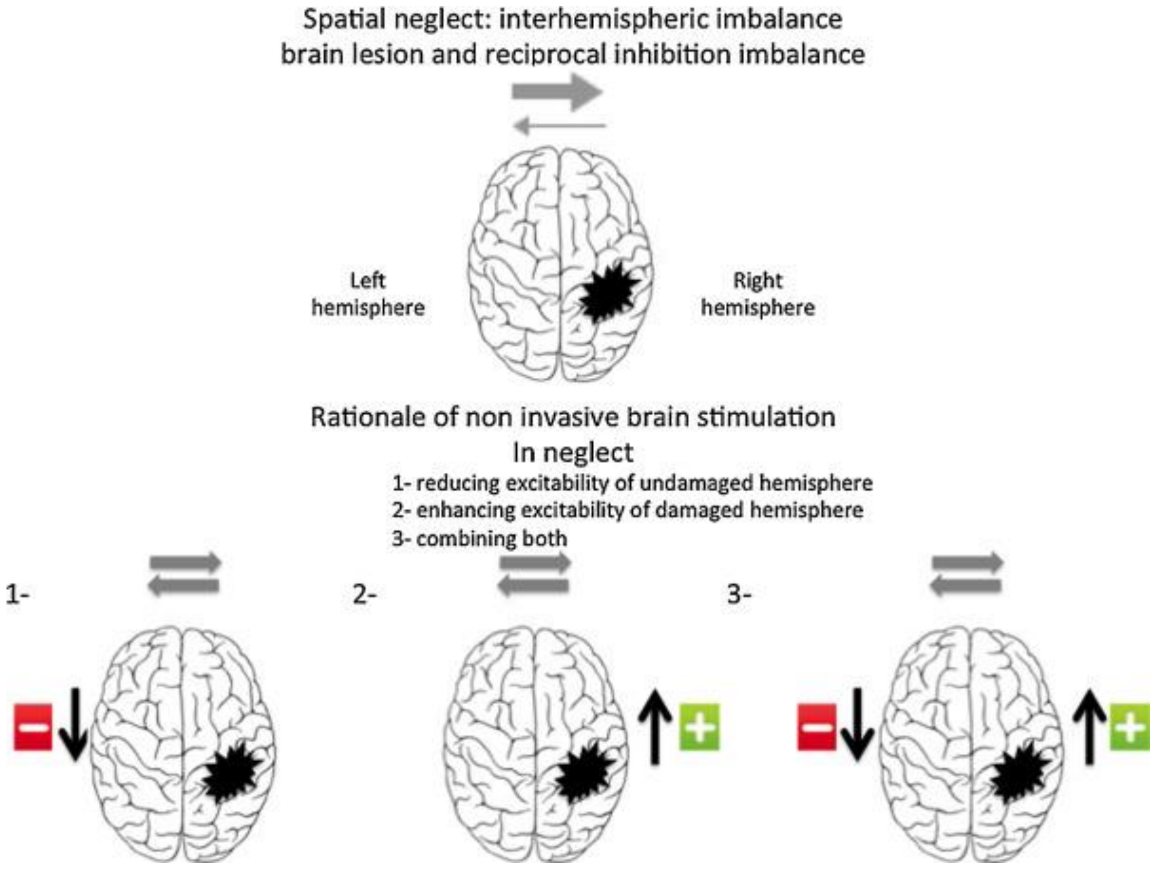


Figure 6 - Interhemispheric imbalance model in spatial neglect and rationale for non-invasive brain stimulation (NIBS). *Spatial neglect is conceptualized as an interhemispheric imbalance resulting from a unilateral brain lesion, leading to reduced excitability in the damaged hemisphere and excessive inhibitory influence from the intact hemisphere.*

Within this framework, NIBS interventions aim to restore functional balance by: (1) reducing excitability of the intact hemisphere via inhibitory stimulation; (2) enhancing excitability of the lesioned hemisphere via excitatory stimulation; or (3) combining both approaches simultaneously. Adapted from Jacquin-Courtois, 2015.

In addition to its clinical applications for patients with neglect, NIBS provides valuable insights into how a healthy brain responds to stimulation. For example, pseudoneglect has been reduced in healthy subjects after receiving high-frequency rTMS over the right postcentral gyrus. The aim of the study was to investigate the processing within the contralateral hemisphere and temporarily rebalance the visuospatial attention system (Fierro et al., 2000). This result has also been replicated by using inhibitory transcranial Direct Current Stimulation (tDCS) over the parietal areas (P6 and P5 according to the 10–20 EEG system). In this latter study, cathodal stimulation was delivered over the right PPC, with concurrent anodal stimulation over the left PPC (Giglia et al., 2011). These findings suggest that temporarily hyperpolarizing the right PPC while depolarizing the left PPC can reverse the leftward bias. Furthermore, these data support the interhemispheric rivalry theory and its implications for allocating visuospatial attention.

In conclusion, empirical evidence seems to support the role of interhemispheric competition in attentional orientation (Marcantoni et al., 2024; Tosoni et al., 2023; Wen et al., 2012). In particular, this has been observed both in neuromodulation studies and in studies observing changes in functional connectivity (FC) following experimental manipulation. However, the study of interhemispheric dynamics is not yet complete or exhaustive.

1.3. Attentional Isolation, Rebound Effects, and Neurochemical Mechanisms

1.3.1. The attentional isolation paradigm

As mentioned briefly in the previous section, and central to this thesis, the *attentional rebound* effect is characterized by an improvement in visual and attentional tracking of target dots in the MOT task, subsequent to an attentional manipulation (Edwards et al., 2021). Specifically, this effect is caused by prolonged lateralization of attentional tracking to one visual field, the attended visual field. Subsequent to the manipulation, a change in tracking performance is observed in the previously unattended, ignored visual field. The attentional rebound effect may reflect different underlying brain mechanisms, ranging from plastic adaptations to a rebalancing of excitatory and inhibitory processes. Edwards and colleagues speculated that attentional rebound may be driven by changes in cortical excitability within specific neural populations. At the cellular level, post-inhibitory rebound spiking has been observed following periods of hyperpolarization (Ferrante et al., 2017; Kuffler & Eyzaguirre, 1955).

A temporary imbalance in neuronal excitability may occur during tasks that engage lateralized regions of the brain asymmetrically (Benwell et al., 2014; Lasaponara et al., 2019). Therefore, the temporary imbalance may exert an inhibitory effect on contralateral brain areas (Ferbert et al., 1992; Perez & Cohen, 2009). A homeostatic control mechanism could mediate improvement in the contralateral ignored visual field after manipulation, in an attempt to rebalance neuronal excitability due to prolonged unilateral attention isolation. This suggests a mechanism of cortical adaptation (Muret & Makin, 2021). Leveraging homeostatic mechanisms might enable the brain to recalibrate its neural circuitry and rebalance changes induced by unilateral isolation in the contralateral, ignored counterpart (Makin et al., 2013). This phenomenon has been observed primarily in the motor system (Goodwill et al., 2012), as well as in human vision (Lunghi et al., 2015) and animal models (He et al., 2006). This process of cortical adaptation likely forms the neural foundation for maintaining the balance between excitation and inhibition, a crucial process indicating cortical plasticity (Tatti et al., 2017; Turrigiano, 2012; Wu et al., 2020). These cortical adaptations are of particular clinical relevance in stroke recovery (Figure 7), where sustained alterations in GABAergic inhibition shape the subacute plasticity window, the brain's endogenous opportunity for repair, and may ultimately determine the degree of functional recovery (Paparella et al., 2023) .

Notably, cortical adaptations have been extensively studied in the motor system. Unilateral training involving one limb results in an increased motor response in the contralateral non-trained limb, in a phenomenon known as *cross education or cross transfer* (Farthing et al., 2007; Hendy & Lamon, 2017; Lee & Carroll, 2007; Ruddy & Carson, 2013). Cortical excitability of the ipsilateral M1 of the trained limb appears to play a crucial role in facilitating improved motor performance in the opposite limb, which has not undergone training (Lee et al., 2010). This phenomenon is thought to involve changes in GABAergic inhibition (see next section), which plays a critical role in mediating the lateralized effects observed in motor function (Andrushko et al., 2023).

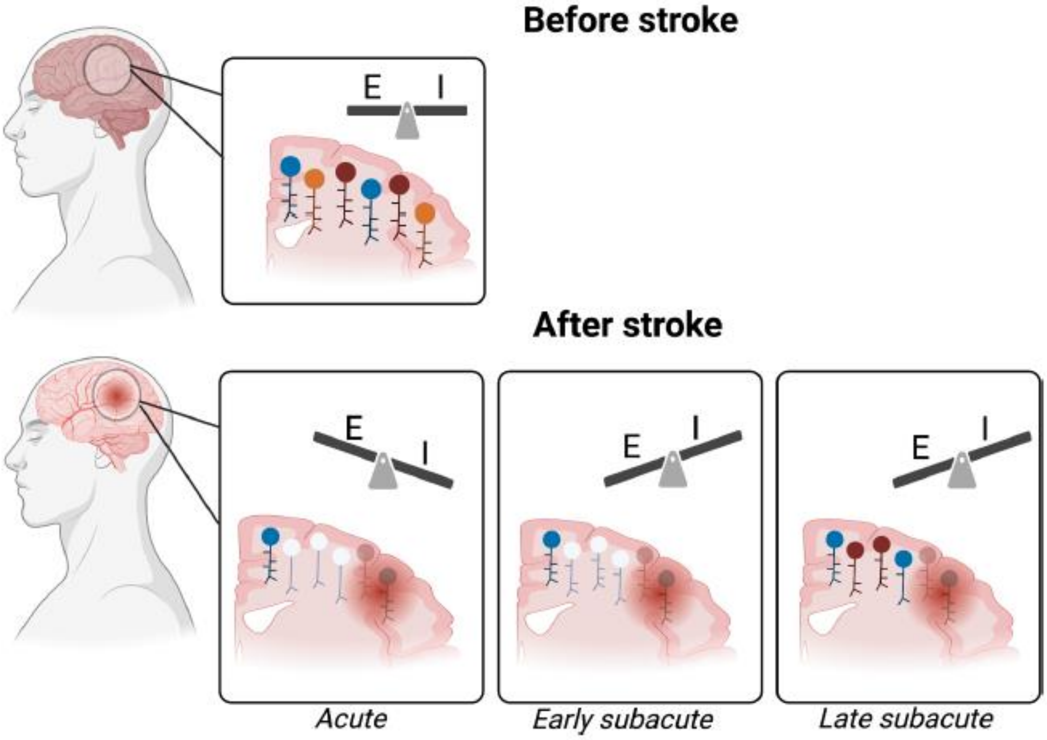


***Figure** 7 - Following stroke, the brain moves through distinct recovery phases: an initial period of neuronal death and excitotoxicity is followed by a shift toward reduced inhibition that promotes the formation of new connections. These connections are subsequently refined as the brain engages in the functional recovery process (Adapted from Paparella et al., 2023).*

Similar results have been found through the use of a monocular deprivation paradigm, with shifts in ocular dominance correlated with changes in GABAergic inhibition in the primary visual areas (Lunghi, Emir, et al., 2015). This enhancement of the deprived eye's function resembles the effect reported by Edwards and colleagues, which indicates an increase in attention towards the visual hemifield that was *ignored* during the isolation phase. We could thus speculate that the lack of enhanced performance in the attended visual field in the Edwards et al study is due to the absence of a homotopic reduction of GABA in the corresponding area recruited during attentional isolation. Furthermore, many training sessions could be necessary to reach a sustained improvement in the attended visual field. Conversely, attentional gain over the ignored visual field, post manipulation, could be a product of changes in GABA levels in brain locations supporting attentional rebound (Frangou et al., 2019).

The neural features of attentional isolation can be investigated through changes in the synchronous neuronal activity of neural populations in parietal areas, particularly in the alpha band (8–13 Hz) - (Doesburg et al., 2009; Sauseng et al., 2005). This could reveal asymmetrical activation of lateralized neural populations in response to attentional isolation and the consequent rebound effect in tracking accuracy. Similar methodologies have been used to classify different types and severities of neglect, and they may be useful for characterizing the neural correlates underlying the attentional rebound (Lasaponara et al., 2021). The characterization of individual differences and of the neurophysiological correlates of attentional isolation and its subsequent rebound may allow these findings to be extended to a clinical setting, particularly in patients with hemineglect (Di Monaco et al., 2011; Moore et al., 2021; Ten Brink et al., 2019; Upshaw et al., 2019; N. Y. H. Yang et al., 2013). Within this framework, transiently exacerbating the neural imbalance between homologous areas in a damaged brain through our manipulation may paradoxically promote rebalancing mechanisms (Figure 7), leading to beneficial effects on visuospatial recovery (Edwards et al., 2022).

1.3.2. Neurochemical basis

GABA (gamma-aminobutyric acid) is the primary inhibitory neurotransmitter in the brain and plays a crucial role in maintaining the balance between excitation and inhibition in visual, motor, and attentional systems. Specifically, GABA exerts a trophic effect that contributes to neuronal growth in the early stages of development and subsequently becomes a key neurotransmitter that regulates the balance between excitation and inhibition in the mammalian brain (Conti et al., 2004; Mortensen et al., 2012; Peden et al., 2008). The role of GABA in regulating intracortical GABAergic inhibition (IGI), a mechanism that shapes cortical receptive fields and subsequent development, is well-documented (Sears & Hewett, 2021). In the visual system, specifically in the retina, three types of GABA receptors have been identified: GABAa, GABAb, and GABAc. In vivo studies in chicks have shown that GABAergic signaling can promote or protect against deprivation-induced myopia. Specifically, the administration of GABAa agonists promotes myopia, while GABAc antagonists enhance protection against it (Schmid et al., 2013).

The development of the visual system is closely linked to the concept of the critical period (CP). CP is defined as the time window during which behavioral experience models and defines the cortex through plasticity mechanisms. Building on this concept, Iwai et al. (2003) investigated when and for how long GABAergic inhibition is required to trigger cortical plasticity. To do so, they selected the GAD65 KO, a (genetically modified) mouse model. These models exhibit reduced GABA release, which has been linked to an absence of effect on ocular dominance (OD) plasticity. However, after administration of diazepam (DZ) - (a benzodiazepine that potentiates GABAa receptor activity), this altered the underlying factors contributing to experience-dependent synaptic modification, setting the brain's readiness window for experience-dependent changes (Iwai et al., 2003). Thus, although the CP appears to close quickly during infancy, paradigms such as monocular deprivation and attentional isolation demonstrate that the chemical balance of cortical plasticity remains susceptible to change.

1.4. Neuromodulation as a Tool for Restoring Interhemispheric Balance

1.4.1. Overview of non-invasive brain stimulation

NIBS is a widely used research technique and, to a lesser extent, a clinical technique for modulating brain activity (Bhattacharya et al., 2022). Specifically, NIBS uses electrical currents or magnetic fields to temporarily excite or inhibit specific brain regions. NIBS has historically been used to treat various pathological conditions, including psychiatric disorders (Brunoni et al., 2018; Milev et al., 2016), neurodevelopmental disorders (Francis et al., 2020), neurological conditions following stroke

(Bonanno et al., 2025; Veldema & Gharabaghi, 2022), neurodegenerative diseases (Oyovwi et al., 2025), substance abuse (Stein et al., 2019), and speech disorders (Han et al., 2024). Some studies have demonstrated the ability of NIBS to identify neurophysiological biomarkers of neurological disease progression (Birreci et al., 2024; Parmigiani et al., 2023). One of the most widely used NIBS techniques is transcranial magnetic stimulation (TMS). The history of NIBS is extensive and spans several decades (for a concise review, see Hamlin & Garman, 2023).

In recent years, there has been a growing application of transcranial electrical stimulation (tES) procedures (Meng et al., 2024; Reed & Cohen Kadosh, 2018; Zeng et al., 2019). In general, tES involves passing a weak direct current through the scalp, resulting in diffuse, subthreshold stimulation of cortical activity. The main types of electrical stimulation identified in the literature are transcranial direct current stimulation (tDCS), transcranial alternating current stimulation (tACS), and transcranial random noise stimulation (tRNS). In tDCS, current flows in a constant manner between a cathode and an anode, and based on the behavioral or physiological effects, researchers typically interpret the cathode as inhibitory and the anode as excitatory. From a physiological point of view, tDCS appears to influence the probability of neuronal activation rather than act on the action potential (A. J. Woods et al., 2016). On the contrary, tACS is mainly linked to the concept of oscillation and frequency (Helfrich et al., 2014; Vossen et al., 2015).

Recently, there has been growing interest in tRNS, an electrical stimulation technique that uses a range of random frequencies (0.1 and 640 Hz). The effects of this stimulation, depending on the parameters, can be excitatory or inhibitory (Moret et al., 2019). The underlying neurophysiological mechanisms are still unclear. However, recent studies have suggested that sodium channel blockers may reduce the changes in cortical excitability produced by tRNS, thereby influencing action potentials in neurons (Potok et al., 2021, 2022; Terney et al., 2008). The application of this technique has expanded considerably over the years as it has been employed in several domains, including motor (Ellena et al., 2025), attention (Contò et al., 2023; Edwards et al., 2020; Tyler et al., 2018), learning (Contemori et al., 2019), vision (Campana et al., 2016), memory, (Murphy et al., 2020) and social cognition (Moreau et al., 2025).

1.4.2. Mechanisms of action

The modulating effect and change in excitability levels following NIBS application have been widely studied over the years. Studies have particularly focused on the ability of brain stimulation to enhance mechanisms associated with brain plasticity that support cognitive processing (Huerta & Volpe, 2009; Thickbroom, 2007; Vlachos et al., 2012). One hypothesis is that these effects are primarily determined by Long Term Potentiation (LTP) and Long Term Depression (LTD) plasticity mechanisms. LTP typically describes an increase in neuronal activation and activity following a period of stimulation, whereas LTD is usually associated with a decrease in neuronal activity and strength. These mechanisms appear to depend on the N-methyl-D-aspartate (NMDA) receptor (Lüscher & Malenka, 2012). LTP and LTD are defined as mechanisms of synaptic strengthening that depend on brain activity (Park et al., 2014).

In recent years, much of the research on electrical stimulation has focused on the concept of entrainment and modulation of brain oscillations. This research has studied the effects of different frequencies on various cognitive domains (Vogeti et al., 2022). However, the entrainment effect appears to depend on neuronal layers, neuron types, and stimulation frequency. This makes it difficult to customize interventions for healthy subjects and patients. In a recent computational study, in order to understand which cells are more directly affected by the stimulation, two metrics were derived using a tACS frequency between 5 and 50 Hz and an electric field amplitude of 0 or 10 mV: membrane polarization length and phase locking value (Gabriel et al., 2025). The authors concluded that excitatory (pyramidal) neurons are more likely to respond to stimulation close to their intrinsic physiological oscillation, while inhibitory interneurons, such as Somatostatin Interneurons (SST) and Parvalbumin Interneurons (PV), are more sensitive to higher-frequency tACS (β–γ range). Consequently, tACS appears to act on network synchronization by promoting mechanisms that enhance the intrinsic oscillation frequency of the network and by changing the excitatory-inhibitory balance in neuronal layers (Agnihotri et al., 2024; Gabriel et al., 2025).

As mentioned above, tRNS shares several characteristics with tACS (Figure 8). However, its mechanisms of action appear to be less well studied, and it has a different neurophysiological substrate (Fertonani & Miniussi, 2017). Technically, the tRNS signal is created from a zero-mean, normally distributed random sequence, where 99% of the values are distributed within ±1 mA. The frequency domain signal consists of equal amplitude coefficients and random phases, leading to a constant power spectrum, characteristic of white noise (Paulus et al., 2016). Evidence reported that tRNS delivered over the Dorsolateral Prefrontal Cortex - DLPFC - results in increased performance on the Attention Network Test (ANT), with a clear impact on speed and accuracy. Authors concluded that tRNS has the potential to affect the cortical executive network (Lema et al., 2021). Facilitatory effects have also been reported in the cortical excitability of the motor cortex (Terney et al., 2008). Applying tRNS to the visual cortex at an intensity optimal for visual processing improves the discrimination performance (Pavan et al., 2019). According to the authors' modeling, the resulting tRNS generates an electric field of 1-3 V/m. While this electric field is insufficient to depolarize cortical neurons directly, it is believed to influence activation probability and modify the depolarization threshold in neurons.

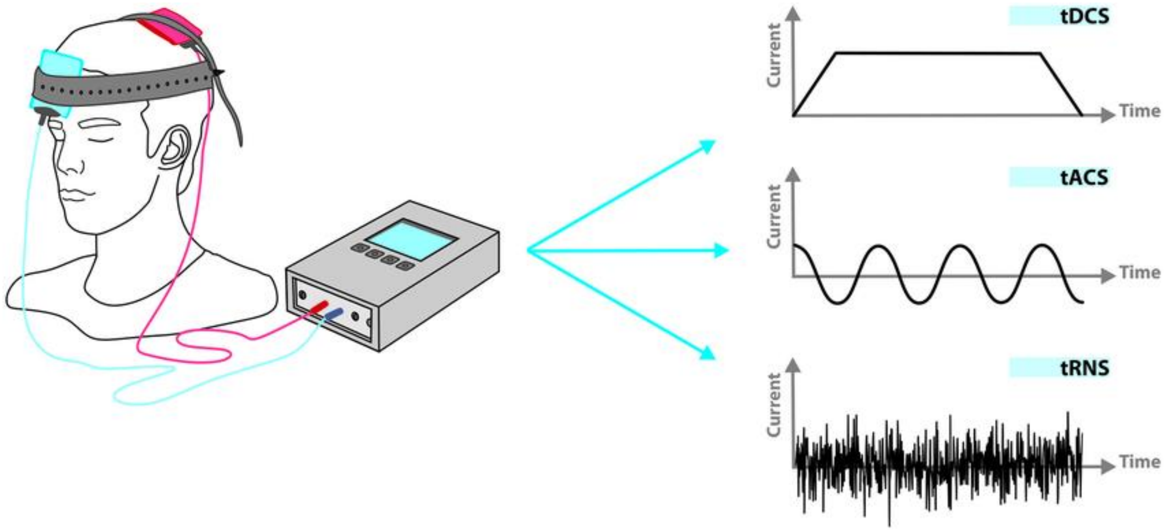


***Figure 8** - Every type of electrical stimulation (tDCS, tACS, tRNS) is associated with a different waveform, with different peak-to-peak amplitude and frequency parameters. Adapted from Yavari et al., (2017).*

Specifically, in the study by Pavan et al., participants were asked to indicate whether two moving patches, presented at slightly different time intervals, moved in the same or different directions. This task provided a sensitive measure of motion discrimination performance. In line with the literature, tRNS was found to exert a neuromodulatory effect, leading to improved performance, indicating that stimulation can enhance the neural processing underlying motion perception. Optimal performance was achieved with a current intensity of 1.5 mA; a higher current level, however, compromised performance (Pavan et al., 2019). Current evidence suggests that "noise in the system" plays a significant role in the neuromodulatory effects of tRNS (Potok et al., 2022; van der Groen & Wenderoth, 2016). This phenomenon, called Stochastic Resonance (SR), is crucial for adapting the optimal stimulation protocol with this technique (Battaglini et al., 2020). Finally, further research is needed to elucidate the role of tRNS and stochastic resonance in promoting long-lasting plasticity changes. This is partly due to the literature's conflicting results (Potok et al., 2022; van der Groen et al., 2022).

1.4.3. Clinical and experimental evidence for attentional modulation of NIBS

NIBS is widely used to modulate visual and attentional processes, with converging evidence showing that it reliably influences brain activity and enhances specific cognitive functions despite an incomplete understanding of its underlying mechanisms (Cazzoli et al., 2010; Giglhuber et al., 2017; Giglia et al., 2011; González-Rodriguez et al., 2022; Harvey & Kerkhoff, 2015; Kashiwagi et al., 2018; Nyffeler et al., 2008; Zebhauser et al., 2019). Rather than providing an exhaustive review, this section offers a concise theoretical framework to contextualize the empirical findings discussed below.

In neurotypical individuals, attentional orienting is thought to be shaped by interhemispheric interactions that favor the left visual hemifield. Consistent with this view, TMS applied over the right AG suppresses the leftward attentional bias induced by small number priming in a line bisection task (Cattaneo et al., 2009). More recent studies have further refined this account by showing that the behavioral impact of stimulation critically depends on the functional connectivity of a distributed network, including the superior temporal, angular, and precentral gyri (Gießing et al., 2020).

Interestingly, functional connectivity is now recognized as a key prognostic marker across several neurological conditions, including hemispatial neglect (Baldassarre et al., 2014; Barrett et al., 2019; Carter et al., 2010; Hong et al., 2019; Kaiser et al., 2015; Wåhlin et al., 2019). Within this framework, NIBS has repeatedly been shown to reshape interhemispheric connectivity, either transiently, immediately after stimulation (Heinen et al., 2017) or through delayed, longer-lasting effects (Battelli et al., 2017). Together, these findings highlight the remarkable plasticity of large-scale brain networks and their capacity to dynamically reorganize in response to targeted neuromodulation.

1.5. Main Research Questions

1.5.1. Overview of study aims

This thesis develops and explores the concept of interhemispheric interaction and cortical adaptation in the visuospatial attentional domain. Each chapter included in the thesis addresses how neuromodulation or behavioral manipulation influences visual and attentional functions, as well as how these changes can be explained by brain plasticity. After a brief theoretical introduction to visual and attentional functions described in this chapter (Chapter 1), the thesis presents a systematic review in Chapter 2. This review examines how NIBS and neuroimaging have been used to investigate visual and spatial attention and how these constructs are closely linked to large-scale brain networks.

More specifically, this review addresses recent literature and discusses how the combined use of these methodologies can improve our understanding of the exact relationship between the brain and attention. This latter multimodal approach is not only fundamental in neurotypical subjects but has also shown promise for clinical populations, particularly those with cerebrovascular lesions and consequent dysfunctions in brain networks. Particular emphasis has been paid to a critical comparative analysis of the results and methodologies adopted by different studies. In addition, this review has sought to highlight the possible criticisms and inconsistencies that are common in studies involving various stimulation protocols related to the study of visual and spatial attention. The review focuses primarily on the most common stimulation techniques adopted in the field of neurostimulation, such as TMS and its variants, tDCS, tACS, and tRNS.

Subsequently, in the first experimental study of the manuscript (Chapter 3), we address the question of how NIBS, particularly tRNS, can be used to study hemispheric asymmetry with an attention isolation procedure. In brief, our results demonstrate a clear hemispheric asymmetry in how frontoparietal tRNS modulates attention reallocation, revealing a measurable and detectable dissociation between the right and left hemispheres. The present study replicated the effect reported by Edwards and colleagues (2021) and further extends it to examine the contribution of each cerebral hemisphere using tRNS on frontoparietal cortical regions. The second experimental study (Chapter 4) investigated the neural correlates of the attentional isolation procedure and the resulting attentional rebound effect. Specifically, neurotypical subjects underwent EEG measurement before, during, and after the attentional isolation procedure to identify possible electrophysiological markers that explain the neural response to the procedure. Finally, we presented a general discussion and final remarks in Chapter 5.

2. CHAPTER 2: From Networks to Cognition - Integrating Brain Stimulation and Neuroimaging to Study Visuo-Attentional Functions

2.1. Abstract

NIBS, when combined with neuroimaging, has been pivotal in studying the causal role of selective cortical areas and networks in human visuospatial attention. The combined approach has enabled detailed investigations of attentional mechanisms, including spatial representation, attention shifts, sustained attention, and feature-based selection, providing the opportunity to modulate and isolate attentional subcomponents and shedding light on their neural underpinnings. However, significant variability persists across studies in terms of design, stimulation protocols, and cognitive paradigms. This systematic review synthesizes converging evidence and outlines six key themes: (1) stimulation of attention network hubs differentially impacts attentional subfunctions; (2) the effects extend beyond focal sites and influence whole-brain organization; (3) stimulation outcomes are strongly state-dependent; (4) white matter micro- and macrostructure constrains individual responsiveness; (5) homeostatic plasticity shapes the trajectory of attentional modulation; and (6) neural oscillations provide a central pathway linking stimulation to behavior.

All data points to the next necessary step: transitioning to personalized, closed-loop stimulation protocols that adapt to ongoing neural activity and individual structural profiles. This shift will allow for the precise mapping of causal dynamics within brain networks and accelerate the development of interventions for disorders involving attentional dysfunctions.

2.2. Introduction

Attention is a fundamental cognitive function that enables individuals to selectively prioritize relevant information while suppressing distractions, thereby optimizing limited processing resources. Over the past few decades, considerable progress has been made in understanding the neural substrates of attention, particularly through the study of large-scale brain networks (S. L. Bressler & Menon, 2010; Sporns et al., 2004). The two main networks linked to attentional functions are the dorsal and ventral attention networks (DAN and VAN; collectively DVAN). These networks play a key role in attentional control by supporting goal-directed (top-down) and stimulus-driven (bottom-up) processes, respectively. Despite extensive research, it remains unclear how dynamic interactions between these networks give rise to flexible and adaptive attentional control.

The aim of this review is to synthesize recent findings on the neural basis and mechanisms of attention, with a specific focus on how NIBS and neuroimaging can be integrated to interrogate visuoattentive functions. Combining NIBS (e.g., -TMS- or -tES-) with neuroimaging techniques, such as fMRI and EEG, offers a unique opportunity to establish causal links between neural activity and behavior. This integrated approach moves beyond correlational descriptions by enabling researchers to perturb specific network nodes or rhythms and measure their behavioral and neural consequences, thus probing the functional organization of attentional networks and their dynamic interactions.

The combination of NIBS and neuroimaging can be implemented in several ways, each providing distinct insights into attentional mechanisms. The most well-established method, which is traditionally associated with conventional NIBS paradigms, is the “perturb and measure” approach (Bestmann & Feredoes, 2013). In this approach, a targeted brain region or network is perturbed, and the subsequent behavioral and neural effects are measured. While this strategy has yielded valuable findings, more recent work has begun to refine stimulation protocols. One line of work uses neuroimaging data to individualize stimulation targets, for example, selecting precise subject-specific sites within a cortical area (Capotosto et al., 2013). Another line uses stimulation parameters tailored to endogenous neural markers, such as the individual's maximum brain oscillation frequency (Kemmerer et al., 2022; Radecke et al., 2023). Other studies have adopted complementary designs, using neuroimaging and stimulation independently to assess the contributions of brain regions to attention (Frank et al., 2020; Jigo et al., 2018). Together, these methodological innovations reflect a shift from coarse, region-based perturbation to more precise, network- and state-informed interventions.

Although several reviews have addressed the intersection of NIBS and neuroimaging in cognitive neuroscience (Bestmann & Feredoes, 2013; Gonzalez-Escamilla et al., 2020; Panico et al., 2020), this review makes a unique contribution by examining how stimulation and imaging techniques converge to elucidate the dynamic architecture of attentional networks. We focus specifically on visuo-attentional functions, emphasizing how causal perturbations of DVAN nodes and oscillations reshape network dynamics and behavior. We highlight the potential of targeted, network-level interventions and critically discuss the limitations of traditional offline stimulation (Capotosto et al., 2013). In particular, we advocate for adaptive, state-dependent stimulation approaches that track ongoing neural activity (Frank et al., 2020) and align interventions with the temporal dynamics of attentional processing. Our review emphasizes the need for temporally precise, network-level interventions that account for the dynamics of attentional processes at different temporal scales and argues that such approaches are essential for both mechanistic insight and translational impact.

These methodological considerations are crucial for addressing a fundamental characteristic of attention: its non-unitary nature. Attention encompasses multiple constructs, including sustained, selective, feature-based, and spatial attention, as well as attentional shifting. These constructs are supported by distinct yet overlapping neural circuits (Figure 9B). An open question is how NIBS influences these specific subcomponents, and under what conditions stimulation effects generalize across different tasks. Additionally, NIBS's efficacy is recognized as state-dependent, meaning that its effects are modulated by ongoing neural activity during stimulation (Hartwigsen et al., 2015; Romei et al., 2016; Silvanto et al., 2007; Silvanto & Muggleton, 2008). Neuroimaging studies have shown that pre-stimulation brain states (Rossini et al., 2015), baseline oscillatory activity (Dugué et al., 2011; Krasich et al., 2022) and individual differences in the brain (e.g., age, sex, and functional connectivity; (Cabeza, 2002; Cabeza et al., 2002; B. Krause & Kadosh, 2014; Vergallito et al., 2022) can predict whether stimulation will enhance or impair cognitive performance. Therefore, understanding state-dependency is critical for optimizing experimental paradigms and advancing personalized neurostimulation protocols aimed at enhancing cognitive abilities or supporting clinical interventions.

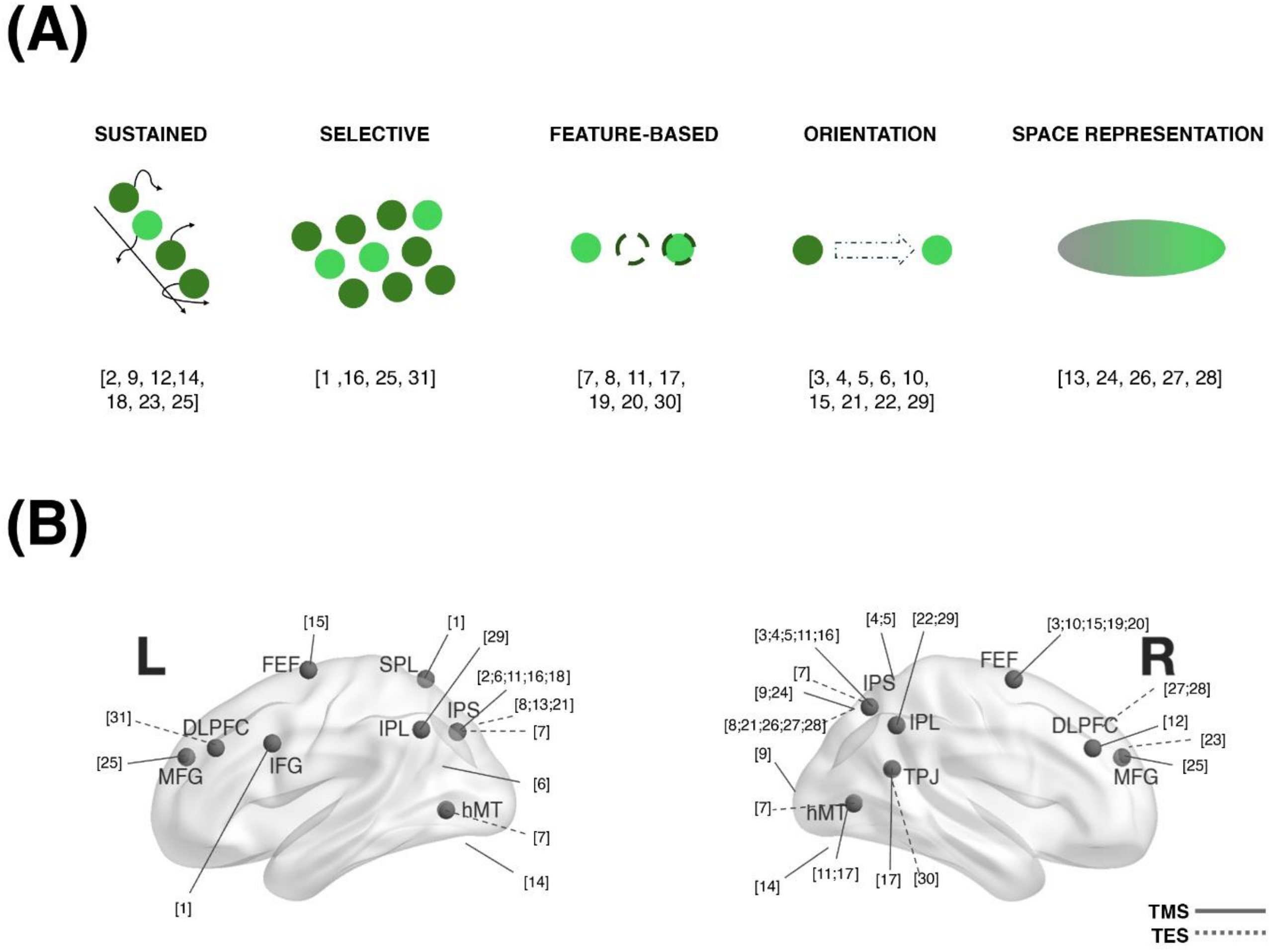


Figure 9: ***Panel (A): Subcomponents of spatial attention.*** *The figure outlines the main subcomponents of spatial attention that emerged in the review. References listed below each subcomponent correspond to studies that primarily focused on each of these distinct, yet interacting, processes. Such subdivision is adopted for simplicity and clarity. It should not be interpreted as an epistemological partition, nor as implying that the subcomponents represent distinct or independently studied scientific entities.* ***Panel (B): Stimulation sites.*** *The figure summarizes the main cortical stimulation sites targeted in the studies included in this review. Solid lines indicate the use of TMS, whereas dotted lines indicate tES. Stimulation sites are shown schematically and should be considered approximate.* ***References:*** *[1] Anderkova et al. 2018; [2] Battelli et al. 2017; [3] Capotosto et al. 2009; [4] Capotosto et al. 2013; [5] Capotosto et al.*

2015; [6] Capotosto et al. 2017; [7] Contò et al. 2021; [8] Di Dona et al. 2024; [9] Frank et al. 2020; [10] Heinen et al. 2017; [11] Jigo et al. 2018; [12] Kazemi et al. 2020; [13] Kemmerer et al. 2022; [14] Liu et al. 2024; [15] Marshall et al. 2015; [16] Mevorach et al. 2010; [17] Painter et al. 2015; [18] Plow et al. 2014; [19] Quentin et al. 2013; [20] Quentin et al. 2016; [21] Radecke et al. 2023; [22] Ramirez-Guerrero et al. 2025; [23] Rostami et al. 2021; [24] Schintu et al. 2021; [25] Song et al. 2019; [26] Tsujimoto et al. 2022; [27] van Schouwenburg et al. 2017; [28] van Schouwenburg et al. 2018; [29] Williams et al. 2024; [30] Wu et al. 2015; [31] Zhang et al. 2022.

This multimodal approach is also important from a translational perspective. By revealing how stimulation reshapes dysfunctional attention networks in a mechanistically informed way, it offers new avenues to personalize rehabilitation strategies and to develop adaptive, closed-loop neurotechnologies for clinical populations. However, there are still significant challenges, such as standardizing methods, improving targeting precision, and translating findings beyond laboratory settings. In the following sections, we first outline our systematic search strategy, then critically review how NIBS–neuroimaging studies have characterized DVAN function, network connectivity, state dependence, white-matter constraints, and attentional lateralization, before turning to a synthetic discussion of conceptual and methodological challenges.

2.3. Materials and Methods

2.3.1. Eligibility Criteria

Studies were selected through a rigorous screening process conducted at the title, abstract, and full-text levels. Articles were screened and selected based on the following criteria: (1) The study had to investigate a subconstruct of visuospatial attention, ensuring relevance to the core topic of attention processes; (2) the use of a brain stimulation technique was mandatory, encompassing interventions such as transcranial magnetic stimulation, transcranial direct current stimulation, transcranial alternating current stimulation, or transcranial random noise stimulation; (3) a neuroimaging measure, such as fMRI or EEG, had to be included to allow for examination of brain activity or connectivity patterns; (4) only original research articles were considered to ensure the inclusion of primary data and findings; (5) articles had to be written in English, allowing for consistency in review and interpretation; (6) studies needed to be peer-reviewed to maintain scientific rigor and credibility; (7) the research had to focus on healthy adult participants, explicitly excluding studies involving children or the aging population to maintain a homogeneous sample relevant to typical adult visuospatial attention processes; (8) Studies involving animal models were excluded to focus solely on human neural mechanisms; (9) Single-case reports were omitted to ensure findings were generalizable to a broader population.

2.3.2. Databases and search strategy

A computer-based search strategy was executed by one author (MT), querying PubMed and Scopus in June 2025. The chosen time period for our search went from 2008 to 2025, focusing on the last 17 years. The following concepts and keywords were used to perform the search on the reported databases:

Concept 1 (Visual attention): *"Attention" OR "Visual attention" OR "Visuospatial attention" OR "Visual field" OR "Bilateral tracking" OR "Biased attention" OR "Spatial orientation" OR "Visual attention" OR "Attentional mechanisms" OR "Sustained attention" OR "Visual perception" OR "Visual processing" OR "Visual search" OR "Spatial attention" OR "Visual spatial processing" OR "Spatial awareness" OR "Attentional allocation" OR "Visuospatial perception" OR "Spatial orienting" OR "Spatial cognition".*

Concept 2 (Brain networks): *"Dorsal Attention Network" OR "Ventral Attention Network" OR "Neural Pathways" OR "DAN" OR "VAN" OR "Brain networks" OR "Neural basis" OR "Brain circuits" OR "Frontoparietal network" OR "Neuroimaging techniques" OR "Imaging biomarkers" OR "Neuroimaging studies".*

Concept 3 (Brain stimulation): *"Transcranial Direct Current Stimulation" OR "Transcranial Magnetic Stimulation" OR "Electrical Stimulation" OR "Transcranial Alternating Current*

Stimulation" OR "Transcranial Random Noise Stimulation" OR "tDCS" OR "tACS" OR "tRNS" OR "TMS".

Each concept was merged with the AND logical operator (Concept 1 AND Concept 2 AND Concept 3). The result of the database investigation returned a total of 1348 articles. Subsequently, duplicates were removed, and 880 articles were admitted to title and abstract screening. To prevent potential biases during the screening procedure and enhance inter-rater reliability, three authors independently assessed the suitability of each article based on adherence to the inclusion criteria. The assessment was based on fairness and adherence to inclusion criteria. Any disagreements in selection or judgment among the authors were resolved through collegial discussion. Out of an initial pool of articles, 85 met the criteria for full-text screening, and ultimately 33 were included in our final review (see Figure 10).

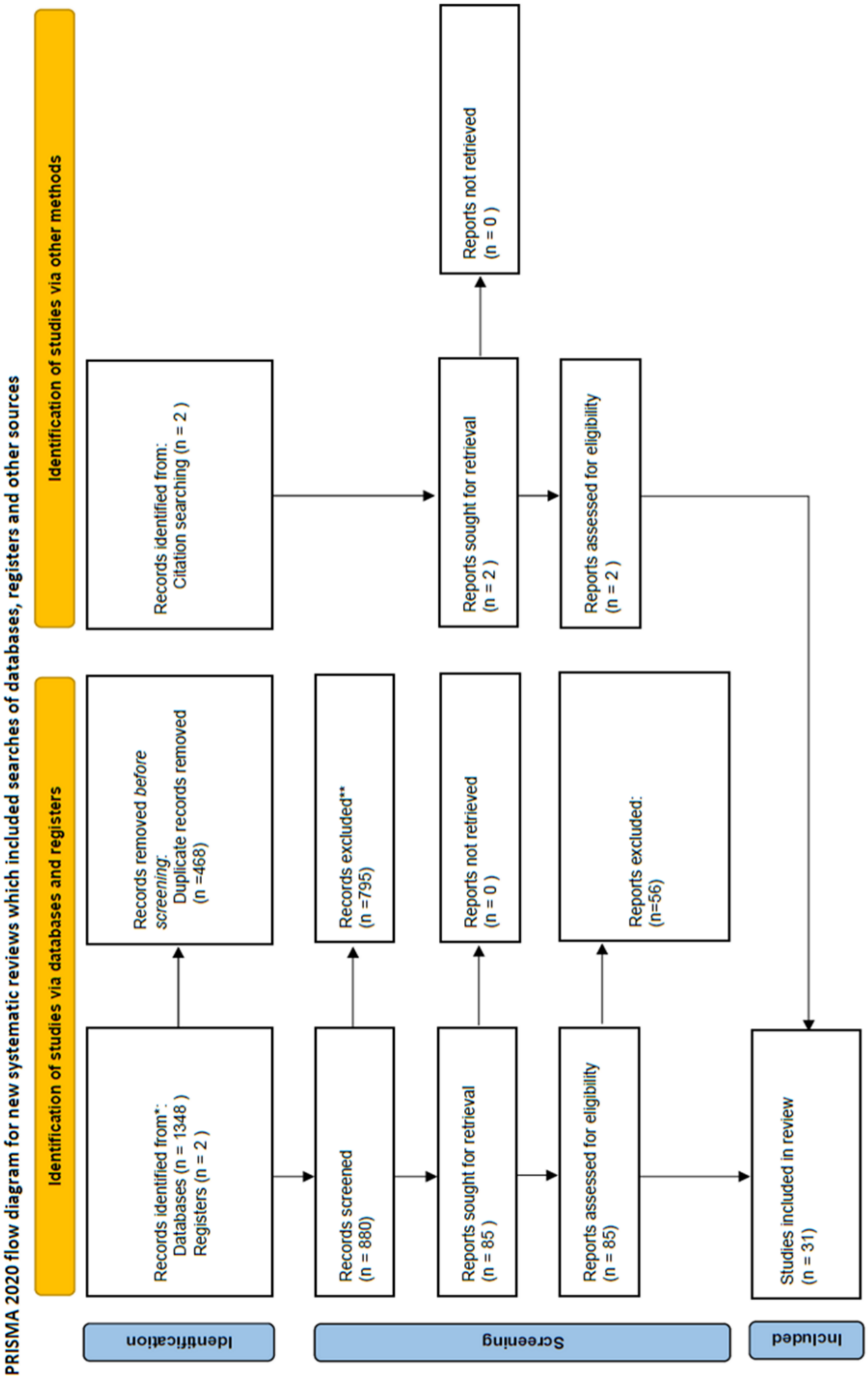

PRISMA 2020 flow diagram for new systematic reviews which included searches of databases, registers and other sources
Identification of studies via databases and registers
Identification of studies via other methods
Identification
Screening
Included
Records identified from*:
Databases (n = 1348)
Registers (n = 2)
Records removed *before screening*:
Duplicate records removed (n =468)
Records identified from:
Citation searching (n = 2)
Records screened
(n = 880)
Records excluded**
(n =795)
Reports sought for retrieval
(n = 85)
Reports not retrieved
(n = 0)
Reports sought for retrieval
(n = 2)
Reports not retrieved
(n = 0)
Reports assessed for eligibility
(n = 85)
Reports excluded:
(n=56)
Reports assessed for eligibility
(n = 2)
Studies included in review
(n = 31)

Figure 10

2.4. Attention networks: interactions within and with other networks

2.4.1. DVAN supports distinct attention functions

Over the past two decades, the study of large-scale brain networks has substantially advanced our understanding of attention as a distributed, dynamic process. Among these, the dorsal and ventral attention networks (DAN and VAN, collectively referred to as DVAN) have been consistently implicated in orchestrating distinct but complementary aspects of attention, enabling adaptive responses to environmental demands. The DAN, predominantly comprising the IPS and the FEF, is primarily involved in top-down attentional control (Corbetta & Shulman, 2002, 2011), whereas the VAN, which includes the TPJ and Ventral Frontal Cortex (VFC), supports the detection and reorienting of attention toward behaviorally salient or unexpected stimuli (Corbetta et al., 2008; Tosoni et al., 2023). Although functionally dissociable, these networks interact dynamically to support flexible attentional control across varying contexts and demands (Vossel et al., 2014). NIBS techniques offer causal tools to interrogate and modulate the functional properties of these attention networks. By targeting specific nodes, NIBS can manipulate neural excitability and oscillatory activity to probe their contributions to attentional performance. Importantly, beyond its transient effects on neural processing, NIBS can induce long-lasting plastic changes (Bhattacharya et al., 2025; Goldsworthy et al., 2015; Huerta & Volpe, 2009). This offers a unique window into the malleability of attentional systems and their potential for therapeutic applications.

Sustained attention, the ability to maintain attention over extended periods, relies on a distributed architecture encompassing both prefrontal and parietal regions. A key hub of this network is the right MFG, which exhibits functional connectivity with both the dorsal and ventral attention networks. In a pivotal study, Song and colleagues (2019) demonstrated that single-pulse TMS targeting the right middle frontal gyrus (MFG) improved sustained attention, hypothesizing that this effect reflects activation of the right hemisphere and facilitation of its connections with other regions, resulting in greater activation of key nodes in bilateral posterior brain areas. Further support for the importance of prefrontal-parietal dynamics in sustained attention comes from studies using rhythmic TMS to target neural oscillations. In a recent study, Kazemi and colleagues (2020) applied rhythmic TMS at alpha and theta frequencies over the right DLPFC, a key region involved in the functions of maintaining focus and goal-driven voluntary attention allocation. Their results revealed behavioral improvements in sustained attention and frequency-dependent modulations of functional connectivity across attention-related networks. Their findings suggest that manipulating the rhythmic activity of prefrontal regions affects broader network dynamics relevant to attentional stability. Similarly, theta-tACS over the Medial Prefrontal Cortex (mPFC) enhanced sustained attention and altered theta-band power distribution across frontal, central, and temporal regions (Rostami et al., 2021), mainly in the right hemisphere. Together, these studies converge on the idea that stimulating highly connected nodes within the attention network can reshape long-range oscillatory dynamics, thereby stabilizing sustained attention performance.

Selective attention-the ability to prioritize relevant stimuli while suppressing distractors relies on top-down filtering mechanisms mediated by the DVAN. Zhang and colleagues (2022) demonstrated that anodal tDCS over the left DLPFC improved distractor suppression, with accompanying changes in regional activity indices, the Amplitude of Low-Frequency Fluctuation (ALFF) in left parietal cortex, and the regional homogeneity (ReHo) in left precuneus, which likely reflect altered integration within attention-related networks rather than simple enhancement of functional connectivity. This result aligns with the work from Contò and colleagues (2021), who demonstrated an improvement in spatial attention performance correlated with enhanced connectivity in the DVAN after multisession tRNS on the IPS. Frank et al. (2020) further demonstrated the causal link between local perturbations and network-wide effects by applying TMS to the parieto-occipital cortex and observing altered connectivity in the parieto-insular vestibular cortex, alongside changes in its interaction with visual areas, which is typically reduced when visual processing is prioritized. The combination of imaging and brain stimulation allowed the authors to evaluate the regulation of activity between networks to reduce potential multisensory information conflict with prevailing visual cues. Mevorach et al. (2010)

investigated how irrelevant stimuli are suppressed, especially when they are more salient than the relevant target. They found evidence of a neural circuit within the DAN that suppresses the processing of salient distractors when attention is directed toward a less salient target, specifically involving the IPS. Ignoring a salient distractor was associated with increased activity in left IPS and decreased occipital region activity, suggesting that the IPS exerts top-down suppression of the early visual cortex. Collectively, these selective-attention studies illustrate how frontal and parietal control regions shape sensory gain in occipital areas, and how NIBS-neuroimaging approaches can reveal both local and distributed changes underlying distractor suppression.

In addition to spatial attention, *feature-based attention*, the ability to selectively process specific attributes such as color, shape, size, or abstract categories, also recruits the dorsal frontoparietal network. Anderkova and colleagues (2018) investigated the short-term effects of the Theta Burst Stimulation - TBS - on cognitive task performance (e.g., the Stroop task), and subsequent changes in resting state functional connectivity within the DAN. A single session of TBS applied over the Left Superior Parietal Lobule - lSPL - enhanced the speed of the Stroop task performance via increased DAN connectivity. In a two-part study, Jigo and colleagues, 2018 first used fMRI to identify frontoparietal regions engaged in feature selection and then applied TMS to causally test their role. They found that neural activity patterns in several frontoparietal areas correlated with task performance. Disrupting the PPC selectively impaired feature-based selection, which supports a causal role for these regions in encoding prioritized visual features. These findings underscore the multifunctional nature of the parietal cortex in attentional selection, demonstrating that nodes classically associated with spatial attention also support non-spatial feature representation.

The VAN, which comprises the TPJ and VFC, activates primarily in response to unexpected yet relevant stimuli (e.g., those that appear outside the spatial focus; Vossel et al., 2014). One open question is whether these nodes also facilitate the reorientation of attention toward specific visual features. Painter et al. (2015) examined how VAN regions influence feature-based attention to address this issue. When visual attention is directed toward a particular feature (e.g., color or shape), neural responses to that feature increase across the entire visual field. This phenomenon is known as *global feature-based* enhancement. Furthermore, when a task-irrelevant stimulus shares the attended feature, it can involuntarily capture attention; this effect is known as *contingent attentional capture*. To explore the causal role of the right TPJ and the right hMT in these attentional effects, Painter and colleagues (2015) applied Intermittent Theta Burst Stimulation (iTBS). They found that stimulating the TPJ did not affect global feature enhancement, attentional capture, or steady state visual evoked potentials (SSVEPs), stimulus-locked oscillatory signals that index top-down visual processing. However, stimulating the right hMT selectively influenced global feature-based enhancement and modulated SSVEPs (Painter et al., 2015). These studies suggest that although TPJ is essential for detecting and responding to unexpected stimuli, it may not directly influence the modulation of feature-based attention. Instead, the parietal, occipital, and extrastriate cortices appear to play specialized roles in prioritizing relevant visual information while mitigating distraction. These interconnected regions work together to dynamically coordinate attentional processes, enhancing perceptual efficiency and goal-directed behavior. Taken together with broader evidence on VAN function, these findings are most consistent with a functional dissociation in which the VAN plays a transient, stimulus-driven role in orienting, whereas dorsal and extrastriate occipito-parietal regions (including hMT) support more sustained, feature-based modulation, although Painter et al. (2015) themselves provide primarily positive evidence for the latter rather than direct causal support for a VAN contribution. Painter et al. (2015) use of SSVEPs further underscores the temporal dynamics of this process by showing how rhythmic neural entrainment reflects the continuous enhancement of task-relevant features modulated by stimulation.

Studies investigating *attentional shifts* between locations or features, as well as the rerouting of information across representations, have consistently observed robust activation of the TPJ. This region is also considered a key region in regulating information from bottom-up and top-down processes. To test this hypothesis, Wu and colleagues (2015) combined tDCS and fMRI in a paradigm that manipulated cognitive load to engage top-down control processes while introducing stimulus-driven surprise to trigger bottom-up attentional responses. They found that the right TPJ was strongly activated when detecting relevant stimuli, yet deactivated during cognitively demanding tasks that required attention. Cathodal tDCS over the TPJ reduced its activity further and increased negative connectivity with the right Middle Occipital Gyrus (MOG) and right FEF, regions linked to bottom-up and top-down control, respectively (Q. Wu et al., 2015). These findings support the idea that the TPJ acts as a switchboard that dynamically reallocates attentional resources through VAN–DAN interactions based on task demands.

Building on this large-scale network perspective, Capotosto et al (2015) used rTMS to demonstrate that distinct subregions of the parietal cortex play specialized roles in attentional shifts. Their study provided evidence of an anatomo-functional subdivision within the parietal cortex, in which different regions of the DAN support either the maintenance or shifting of attention. Specifically, rTMS over the vIPS impaired the maintenance of attention, whereas stimulation over the mSPL affected the shifting of attention. These findings support a model in which distinct yet interconnected parietal hubs facilitate complementary attentional processes, allowing for both stability and flexibility in visual selection. Heinen et al (2017) investigated the contribution of specific cortical hubs to the coordination of inter-network dynamics, given the continuous functional interaction between the DAN and the VAN during visuo-attentive shifting. To this end, they employed a TBS protocol in conjunction with fMRI during a cued visuospatial attention task. Their results showed that FEF stimulation disrupted attentional shifts, particularly affecting the ability to disengage from the current focus. Notably, during attentional shifts, TBS to the right FEF suppressed neural activity in the bilateral SMG and impaired functional connectivity between the right FEF and SMG. These findings suggest that the right FEF, a core region of the DAN, facilitates attentional shifts by modulating its connectivity with the SMG in the VAN, thereby supporting disengagement from the current focus of attention. These studies highlight that shifting, maintaining, and reorienting attention are mediated by partially segregated yet interacting frontoparietal hubs, whose causal contributions can be dissected with stimulation-imaging approaches.

Together, the reviewed studies illustrate that attentional performance emerges from the coordinated activity of functionally specialized hubs distributed across the DVAN. The crucial role of the DVAN in sustaining, filtering, and shifting attention is clear, as different regions have distinct yet overlapping functional contributions. This growing body of evidence supports the idea that the attentional system is both modular and integrated. Distinct regions underpin specific attentional subprocesses, yet their functional output depends on flexible network interactions.

2.4.2. Network connectivity changes result in performance changes

Having outlined the distinct contributions of the DAN and the VAN to specific attentional subprocesses, we next consider how changes in their connectivity (e.g., the functional coupling that reflects how tightly these networks co-activate and exchange information) can directly translate into measurable performance outcomes. This section reviews evidence that modulation of network interactions, particularly via NIBS, can directly shape attentional performance. By altering the dynamics within and between attentional networks, NIBS provides a way to investigate the causal relationship between network-level communication and cognitive function.

Multiple studies suggest that transcranial stimulation not only enhances behavioral performance but also induces changes in large-scale network connectivity (Contò et al., 2021; Gold et al., 2022; Momi et al., 2023). This supports the view that these attention networks play a causal role in cognitive control. For example, Anderkova and colleagues (2018) demonstrated that applying iTBS to the lSPL increased connectivity in the DAN and with improved cognitive speed, as demonstrated by faster responses in the Stroop task. Their findings highlight how targeted neuromodulation can strengthen the functional integration of regions related to attention, thereby optimizing cognitive control processes. Other forms of stimulation, such as tDCS and tRNS, have also been shown to influence attentional performance through network-level mechanisms. For example, Zhang et al. (2022) found that tDCS over the left DLPFC enhances distractor suppression, with behavioral gains covarying with changes in ALFF and Regional Homogeneity (ReHo) in parietal and midline regions that are embedded within the broader DAN rather than with explicit measures of long-range functional connectivity. Similarly, Contò et al. (2021) showed that tRNS over the IPS improved spatial attention, and participants demonstrated greater accuracy in spatial discrimination tasks. Neuroimaging data from both studies revealed that stimulation modulated local brain states and functional connectivity across broader, more distributed networks. This suggests that behavioral gains are tightly linked to large-scale network reorganization, although the precise directionality of connectivity changes (e.g., compensatory vs. facilitation) often remains difficult to infer from resting-state measures alone. Complementary evidence comes from work specifically examining how rTMS to the parietal cortex reshapes large-scale dorsal attention networks during visuospatial tasks. Plow et al. (2014) applied offline 1 Hz rTMS to the left IPS and used fMRI during bilateral visual tracking to show that disrupting a single parietal node produces widespread changes in BOLD activity across parietal, temporal, and occipital regions in both hemispheres. Their results supported an interhemispheric "push–pull" dynamic: activity decreased in the stimulated IPS and its ipsilateral synergists (e.g., Inferior Parietal Lobule (IPL), while homologous regions and medial parietal areas, Superior Parietal Lobule (SPL) and precuneus, showed increased activation.

Critically, the evolution of these activation patterns over time related to changes in tracking accuracy, suggesting that compensatory recruitment of distributed network nodes helps counteract the behavioral impact of IPS perturbation. Extending this approach, Battelli et al. (2017) reanalyzed the same dataset, focusing on cortico–cortical functional connectivity among key dorsal attention nodes (IPS, FEF, hMT+). They demonstrated that inhibitory rTMS to left IPS induces immediate reductions in functional connectivity between the stimulated IPS and ipsilateral dorsal attention regions, followed by delayed increases in interhemispheric and long-range connectivity. The magnitude and temporal profile of these connectivity changes strongly predicted individual tracking performance, directly linking dynamic reconfiguration of network integrity to the behavioral consequences of parietal stimulation. Together, these studies provide compelling evidence that NIBS acts by reshaping both local and long-range interactions within the dorsal attention network, and that the time course of these connectivity changes is a critical determinant of attentional performance.

These findings raise important questions about the mechanisms linking neural connectivity and cognitive enhancement. Interestingly, inhibitory stimulation protocols, such as cathodal tDCS, have been shown to paradoxically increase connectivity rather than suppress it (Tsujimoto et al., 2022). One possible explanation is that neuromodulation affects the signal-to-noise ratio within the stimulation regions, effectively reducing local neuronal noise and fostering greater synchronization with distant brain areas. These mechanisms could also account for the widespread effects of focal stimulation, including connectivity changes in non-targeted regions and behavioral improvements observed during resting-state periods (Contò et al., 2021; Tsujimoto et al., 2022). Collectively, these findings indicate that, when precisely targeted and tuned, transcranial stimulation can effectively modulate attention networks. This has promising implications for clinical interventions in neurorehabilitation but also underscores that inhibitory and excitatory labels for NIBS protocols are overly simplistic at the network level.

2.5. State Dependent effects of NIBS

An important emerging insight from studies combining NIBS and neuroimaging is that the effectiveness of brain stimulation depends not only on where and how it is applied, but also on the ongoing neural activity within the targeted network. The state dependency hypothesis of NIBS posits that moment-to-moment fluctuations in neural activity, whether driven by shifting task demands (e.g., tracking a moving target or responding to a sudden salient event) or intrinsic network dynamics, can significantly impact how stimulation influences neural activity and behavior (Bestmann & Feredoes, 2013; Mazzoni et al., 2017). Seminal conceptual and empirical work (Bestmann & Feredoes, 2013; Silvanto, 2008) has further articulated how the pre-stimulation brain state and ongoing task engagement constrain both the sign and magnitude of NIBS effects in visual and higher-order cortex, providing a unifying framework for many of the task- and phase-specific findings reviewed here.

Visuospatial attention is a particularly clear example of this principle. As attention prioritizes processing in specific regions of the visual field, distinct neural states are created that determine how stimulation interacts with neuronal populations. Consequently, the impact of NIBS is modulated by several factors, including the current spatial focus of attention, the engaged sensory modality, and the specific stimulus features being processed during a task. This helps explain why stimulation effects are often most pronounced during active task performance as opposed to rest. The strongest modulations occur in network nodes that are actively engaged in the ongoing cognitive process.

Research examining task-specific effects is crucial for understanding the functional dynamics of the DVAN, especially how brain stimulation modulates its contribution to attentional control based on task demands. For instance, Heinen et al. (2017) demonstrated that FEF plays a key role in mediating shifts in visuospatial attention, particularly during tasks requiring frequent reorientation of attentional focus. Specifically, in their study, stimulation only affected performance during the task conditions that required attentional reorientation, not during other phases of the task. Interestingly, the FEF–SMG network was functionally engaged only during attentional shifts, such that stimulation produced measurable effects exclusively when this circuitry was active. In contrast, the absence of TBS effects on the TPJ and IFG suggests a state-dependent mechanism, though this is reflected by a lack of modulation rather than its presence. These regions are typically recruited in response to expectation violations, such as invalid cueing, which were absent in the current task design. Consequently, the TPJ and IFG were not functionally engaged under the present task conditions, rendering them unresponsive to stimulation. This further underscores the state-dependent responsiveness of distinct nodes within the DVAN.

Consistent with these findings, Contò et al. (2021) showed that multi-session tRNS combined with task training can improve the DVAN response and task performance. However, these improvements are task-specific and do not necessarily transfer to different attentional tasks. Behavioral improvements and changes in DVAN connectivity occurred only when tRNS was applied to task-relevant areas (e.g., the parietal cortex) during training. This suggests that engaging specific attentional processes in an ongoing cognitive state was necessary for stimulation to produce measurable effects. Moreover, despite both tasks (temporal and orientation judgment) engaging overlapping visual regions at baseline, only the task involving spatial attention improved when paired with tRNS. These results suggest that stimulation effects depend on the degree to which the targeted region is involved in the task being trained. These findings highlight the adaptability and the inherent constraints of DVAN modulation through NIBS interventions. Furthermore, studies such as Song et al. (2019) emphasize the MFG's role in mediating between sustained and selective attention based on task demands.

Similar further findings emerged from the current literature (M. Liu et al., 2024). They showed that cTBS applied to the left or right IPL induces strongly state-dependent network responses: during rest, stimulation facilitated large-scale network coupling, whereas during task performance, it primarily reduced between-network connectivity in domain-specific, task-active networks, despite leaving behavioral performance unchanged. These findings align with the view that IPL functions as a flexible hub whose perturbation triggers compensatory network reorganization rather than overt behavioral disruption. Additionally, M. Liu et al (2024) revealed a clear state-dependent effect of cerebellar iTBS in their study, with significant neural and behavioral changes observed only during the eyes-open condition. Specifically, enhancements in EEG power (in the theta and alpha bands), functional connectivity, and network efficiency emerged exclusively during the eyes-open condition, while the eyes-closed condition showed no significant modulation. This highlights that iTBS interacts with ongoing brain states and is more effective when attentional systems are externally engaged.

Together, these findings demonstrate that the effects of NIBS are not uniform. Instead, they propagate through networks in a way that depends on the specific attentional features, sensory modality, or location engaged. This state-dependent property makes brain stimulation both a powerful tool for investigating the mechanisms of visual attention and a promising approach for selectively modulating neural activity within the DVAN. Accumulating evidence highlights the remarkable adaptability and inherent constraints of using NIBS to modulate attention networks. This emphasizes the need for careful consideration of brain state in both research and potential clinical applications, and suggests that closed-loop protocols that explicitly monitor and explain ongoing state may be necessary to achieve reliable and replicable effects.

2.6. The Role of White Matter Pathways in Mediating Neurostimulation Effects on Attention

Recent advancements in brain stimulation research have begun to reveal the significant role of white matter pathways in modulating attentional processes. This challenges the traditional emphasis on cortical excitability alone. A growing body of research now suggests that the efficacy of neurostimulation in enhancing attention and visual processing depends not only on directly stimulating cortical regions, but also on the integrity and connectivity of underlying white matter tracts. In this framework, “connectivity” does not simply refer to functional co-activation, but to the anatomical properties of white matter pathways (their presence, strength, and microstructure) which constrain how stimulation-induced activity propagates through attention networks. Measures such as tract probability, Fractional Anisotropy (FA), and Hindrance Modulated Orientational Anisotropy (HMOA) index how efficiently different nodes of the attention network can communicate and increasingly appear as key determinants of stimulation outcomes.

Quentin et al. (2013) provided evidence showing that the behavioral effects of TMS on visual attention depend on structural properties of long-range white matter pathways. In their study, TMS over FEF enhanced visual detection, but the magnitude of this enhancement varied across individuals and was negatively correlated with the structural connectivity of a fronto-tectal pathway linking the FEF to the superior colliculus. Individuals with weaker connectivity showed larger TMS-induced facilitation. Rather than reflecting cortical excitability alone, these findings suggest that stimulation effects are shaped by the architecture of attentional circuits and that white matter pathways can constrain or amplify the propagation of TMS-evoked signals across the network. This study underscores a fundamental shift in our understanding of how attention can be modulated by brain stimulation. It emphasizes that the success of these interventions also depends on specific white matter connections linking frontal areas involved in top-down control with subcortical regions responsible for processing visual information. By identifying the fronto-tectal pathway as a critical mediator of these effects, the study by Quentin et al. (2013) provides novel insight into how visual detection can depend on underlying structural pathways, that is, on the anatomical network in which it is embedded. This represents a significant departure from the traditional view that attributes such improvements to cortical changes only. It expands the scope of neurostimulation research to include the role of white matter connectivity in shaping cognitive outcomes.

Building on this integrative view, Quentin et al. 2016 extended their investigation to examine the impact of neurostimulation on visual contrast sensitivity, a critical component of visual perception, and its correlation with brain activity and white matter structure. Using rhythmic 30 Hz (high-beta) TMS over the right FEF, they demonstrated a frequency-specific, causal leftward shift of the contrast sensitivity function, reflecting a contrast-gain mechanism. Importantly, diffusion imaging revealed that individual differences in the stimulation-induced facilitation were positively correlated with microstructural integrity in the frontoparietal pathway connecting the FEF with the IPS. This finding is significant because it suggests that interindividual variability in the behavioral effects of rhythmic neurostimulation is partly explained by differences in white matter microstructure. In particular, the microstructural integrity of the right frontoparietal pathway appears to shape how effectively high-beta stimulation can modulate visual sensitivity. This work highlights the importance of considering white matter microstructure when evaluating the efficacy of brain stimulation techniques and supports the idea that individual differences in tract properties may serve as predictors of responsiveness to neurostimulation. In contrast to Quentin et al. (2013), here stronger tract microstructure amplified the behavioral effect of stimulation, consistent with the notion that efficient frontoparietal connectivity supports the entrainment of top-down attentional signals. Together, these two studies demonstrate that distinct white matter pathways can either limit or enhance stimulation effects depending on their role within the relevant cognitive network.

Schintu et al. (2021) further emphasized the role of white matter connectivity in how parietal inhibitory stimulation reshapes attentional networks. In healthy participants, cTBS over the right PPC produced a neglect-like rightward bias and altered RSFC, increasing coupling between the right PPC and the left superior temporal gyrus. Crucially, the magnitude of these RSFC changes was inversely correlated with FA in the posterior corpus callosum connecting the two PPCs**:** participants with higher callosal FA showed smaller TMS-induced connectivity changes. This suggests that robust callosal pathways stabilize interhemispheric attentional dynamics, limiting the degree to which inhibitory stimulation perturbs the network (Schintu et al., 2021). This highlights the critical role of white matter architecture in shaping both functional and behavioral effects of TMS and underscores the need to incorporate interhemispheric connectivity into mechanistic models of neurostimulation effects on spatial attention.

A recent study by Ramírez-Guerrero et al. (2025) further advances this network-based view of neurostimulation by examining how individual differences in white matter microstructure shape susceptibility to TMS-induced changes in spatial attention. In this study, the authors applied online TMS to the right inferior parietal lobule (rIPL) while participants performed a near-threshold detection task under endogenous or exogenous cueing. Although rIPL stimulation did not modulate conscious perception per se, it produced attention-specific behavioral effects, including reduced accuracy during endogenous orienting and faster responses to right-hemifield targets, mirroring the right-lateralized organization of attentional networks. Crucially, interindividual variability in these TMS effects was systematically related to the microstructural integrity of long-range association fibers, particularly the SLF branches and the inferior fronto-occipital fasciculus IFOF. Specifically, reduced HMOA in left SLF I and II predicted stronger TMS effects, consistent with compensatory or competitive interhemispheric mechanisms, whereas higher integrity in left superior longitudinal fasciculus (SLF) III predicted larger stimulation effects, suggestive of enhanced signal propagation through pathways feeding the stimulated region. Additional correlations between attentional orienting (in the control condition) and white matter integrity across SLF II–III and the inferior fronto-occipital fasciculus (IFOF) further highlight the structural organization of attention networks. Together, these findings demonstrate that white matter microstructure is a key determinant of both attentional performance and susceptibility to neuromodulation, reinforcing the need to incorporate individual connectivity profiles into mechanistic models and personalized stimulation protocols.

Taken together, these studies represent a significant shift in our understanding of how brain stimulation influences attention and related cognitive processes. Moving beyond the traditional view that focuses exclusively on cortical excitability, they highlight the critical role of white matter tracts in modulating the effects of stimulation and network changes. White matter integrity emerges as a key determinant of neurostimulation outcomes, whether indexed by anatomical connectivity (Quentin et al., 2013), microstructural organization-based measures (Quentin et al., 2016; Ramírez-Guerrero et al., 2025), or anisotropy (Ramírez-Guerrero et al., 2025; Schintu et al., 2021). This evolving perspective suggests that the effects of stimulation on attention are not confined to the targeted cortical regions but are also shaped by the quality of the underlying white matter networks connecting these regions. Collectively, these studies advance our understanding of the effects of neurostimulation on attention by shifting the focus from isolated cortical regions to the critical role played by white matter tracts in mediating and modulating these effects. This complexity emphasizes that white matter tracts are not passive conduits but active determinants of how stimulation reshapes cognitive networks. As such, a comprehensive mechanistic model of neurostimulation must integrate both gray matter targets and white matter pathways, recognizing that the structural architecture of attention networks constrains - and sometimes predicts - the behavioral impact of neuromodulation. This emerging perspective lays the groundwork for more personalized stimulation interventions, in which individual connectivity profiles guide target selection, protocol choice, and treatment expectations.

2.7. Interhemispheric (im)balance and neuromodulation in the lateralization of visuospatial attention

The lateralization of visuospatial attention stems from asymmetric interhemispheric dynamics. Competing processes between the two hemispheres generate a perceptual bias that typically favors the left visual field. This intrinsic imbalance is observed in both cerebrovascular patients and healthy individuals alike and reflects a core principle of attentional organization. It also represents a key target for neuromodulatory interventions. Initially described in patients with hemispheric lesions showing hypoactivity in the damaged side and compensatory hyperactivity in the intact hemisphere, this asymmetry manifests in neurotypical individuals as subtle "pseudo-neglect". Converging evidence from prism adaptation paradigms (Panico et al., 2020) indicates that visuo-motor realignment can recalibrate these asymmetric frontoparietal networks, offering a complementary behavioral route, alongside NIBS, to rebalance pathological attentional biases in neglect and related syndromes.

Studies on neuromodulation highlight the causal role of parietal regions in shaping these biases. Schintu et al. (2021) showed that inhibitory TMS over the right PPC induced a rightward attentional shift and increased RSFC between right IPS and left STG. These effects were modulated by interhemispheric PPC integrity. Similarly, Tsujimoto et al. (2022) found that bilateral tDCS (right inhibitory, left excitatory) produced slower responses to left-sided targets, increased RSFC in the right DAN, and decreased connectivity in the right VAN. These findings indicate that local PPC perturbations drive the network-level reorganization that underlies attentional asymmetries. Domain- and hemisphere-specific contributions have also emerged. Right MFG stimulation enhances sustained attention, possibly via bilateral posterior connectivity, whereas visual and selective attention rely on left-lateralized frontoparietal circuits (Song et al., 2019). Right IPL stimulation disrupted attentional processing, while left IPL stimulation selectively affected semantic tasks, supporting hemispheric specialization (Williams et al., 2024). Within the DAN, right ventral intraparietal cortex (vIPS) mediates spatial allocation, whereas medial superior parietal lobule (mSPL) supports attentional shifting (Capotosto et al., 2013). Frequency-specific interventions further refine this picture. Right-lateralized alpha-tACS has been reported to induce a leftward attentional shift with increased intra-hemispheric alpha coherence (van Schouwenburg et al., 2018), although later work from the same group failed to find differential effects of synchronous versus desynchronous alpha-band stimulation (van Schouwenburg et al., 2017), underscoring the fragility of these effects and the importance of replication.

Oscillatory-tuned tACS appears to be central to these dynamics. IAF-tACS over the left parietal cortex enhances left-hemifield discrimination during covert attention (Radecke et al., 2023). In contrast, IAF-tACS over the left temporoparietal cortex induces transient shifts in alpha lateralization (lasting 1 minute) and corresponding transient changes in attentional bias, with no sustained effects across the full post-stimulation period. Critically, these effects disappear at non-matched frequencies (Kemmerer et al., 2022). Overall, attentional lateralization emerges from the interplay of interhemispheric interactions and frequency-specific neuromodulation. The interplay reflects the flexibility of attention networks in shaping spatial biases but also reveals that frequency-tuned interventions may have limited temporal windows of efficacy, which have important implications for experimental timing and clinical translation.

2.8. Oscillations as drivers of attentional bias

Neural oscillations offer a dynamic framework for understanding the temporal organization of attention. Large-scale network models delineate the anatomical substrates of attentional control, while oscillatory activity captures the real-time coordination of these processes. Alpha-band oscillations (8–13 Hz) have received particular attention for their role in modulating sensory excitability in anticipation of task-relevant stimuli. Alpha desynchronization, particularly in the visual cortex, is consistently observed during covert spatial attention and reflects a release from inhibition that facilitates enhanced processing. Beyond correlational evidence, NIBS techniques such as tACS and rhythmic TMS allow for the causal probing of oscillatory function by directly interacting with endogenous rhythms.

Capotosto et al (2009) demonstrated that anticipatory parieto-occipital alpha desynchronization, which is jointly regulated by the FEF and IPS within the DAN, is critical for target discrimination. Building upon this finding, task- and region-specific effects emerged. IPS stimulation disrupted alpha during visuospatial tasks, while AG stimulation affected semantic tasks (Capotosto et al., 2017). This revealed a functional dissociation within the parietal cortex. Further research has shown that right mSPL stimulation reduces high-alpha desynchronization and impairs shifting; vIPS stimulation suppresses contralateral low-alpha and impairs attentional maintenance; and right FEF stimulation modulates contralateral alpha, consistent with the interhemispheric competition framework (Capotosto et al., 2015; Marshall et al., 2015).

Based on this framework, Liu et al., (2024) found that, after three sessions, one week of bilateral cerebellar iTBS enhanced multi-task attentional performance, accompanied by increased alpha/theta power and altered functional connectivity. AEC-based network metrics (e.g., clustering coefficient, global efficiency) tracked behavioral gains, indicating frequency- and state-dependent modulation of large-scale networks. Similarly, alpha-frequency tACS shows frequency-specific effects that benefit from personalization to the individual's alpha frequency (Kemmerer et al., 2022; Radecke et al., 2023), though there are still inconsistencies (van Schouwenburg et al., 2017, 2018). A recent systematic review by Klink et al., (2020) emphasizes this heterogeneity across cognitive domains and highlights the roles of montage, intensity, and individualized frequency tuning in determining whether tACS produces robust behavioral and neural effects, cautioning against overly general conclusions from single positive studies. Beyond alpha, Rostami et al. (2021) showed that theta tACS over the medial prefrontal cortex increased frontal-midline theta, strengthened DAN connectivity, and improved sustained attention. Sources were found in the mPFC and anterior cingulate. Similarly, Kazemi et al. (2020) reported that alpha- and theta-rTMS enhanced rapid visual information processing (RVIP) performance by suppressing irrelevant and engaging task-relevant regions. More specifically, alpha-frequency rTMS over the right DLPFC produced the most robust behavioral improvements and was associated with increased theta-band lagged nonlinear connectivity between right DLPFC and left IPL, alongside broader DAN–DMN network reorganization, whereas theta-frequency stimulation produced weaker and more spatially restricted effects (Kazemi et al., 2020). Di Dona et al., (2024) found that parietal beta tACS improved visual discrimination and selectively reduced FOOOF-corrected beta power. Frontoparietal or sham stimulation had no effect.

Together, these findings suggest that neural oscillations, especially alpha, theta, and beta, play a causal, topographically specific role in visuospatial attention. NIBS enables the dissociation of contributions from frontal, parietal, and cerebellar nodes to processes such as shifting, allocation, and maintenance. Moreover, tailoring stimulation to individual oscillatory profiles often yields stronger network and behavioral effects than standardized approaches, underscoring the importance of personalized, frequency-specific neuromodulation. At the same time, the mixed tACS literature reminds us that oscillatory entrainment is constrained by anatomy, brain state, and stimulation parameters, and cannot be assumed to produce uniform or robust attentional benefits.

2.9. Discussion and future directions

This review synthesized the current state of research on visuospatial attention, which uses integrated NIBS and neuroimaging methodologies, with a particular emphasis on how causal perturbations of DVAN nodes and oscillations reshape network dynamics and behavior. Visuospatial attention is a broad construct that relies on distributed cortical and subcortical networks to allocate processing resources dynamically during tasks that require such cognitive function. By combining NIBS with neuroimaging, researchers can probe the causal mechanisms underlying attentional control. This allows them to move beyond traditional correlational approaches and into frameworks capable of elucidating network-level dynamics and behavioral outcomes. Throughout this review, we critically examined current methodologies, changes in network connectivity, and behavioral consequences. We also explored interhemispheric balance and assessed neural oscillations as mediators of attentional processes. Furthermore, we considered the role of structural differences in response to NIBS and how these differences may directly affect behavior.

This review reveals the broad and heterogeneous landscape of studies in the visuospatial attention domain. Over the last decade, NIBS techniques have evolved from relatively simple "perturb-and-measure" paradigms into integrated methodologies that incorporate neuroimaging and NIBS. This evolution enables more tailored interventions for individual participants. Combining NIBS and neuroimaging provides a substantial framework to examine brain network dynamics and behavioral outcomes, highlighting their long-standing mutual relationship. Recent advances have expanded this integration to include stimulation protocols that incorporate real-time neuroimaging and closed-loop systems, increasing mechanistic insight and potential efficacy. However, the field remains methodologically heterogeneous, with significant variability in stimulation protocols, targeted brain regions, and behavioral paradigms. Such inconsistencies highlight the critical need for individually calibrated protocols and standardized methodologies to ensure reproducibility and to facilitate translation into clinical applications. A key message of our synthesis is that the same nominal protocol can have very different network and behavioral consequences depending on timing, brain state, and structural connectivity, which complicates the efforts to aggregate findings across studies.

One of the main challenges for NIBS in the context of attention research is targeting the specific subcomponents of this non-unitary cognitive construct. This review emphasizes that activating nodes within the dorsal and ventral attention networks can influence specific attentional processes, such as sustained attention, selective attention, feature-based attention, spatial representation, and attentional shifts. This finding is consistent with previous studies that have demonstrated the complementary roles of these networks in flexible attentional control (Corbetta & Shulman, 2002; Vossel et al., 2014). In this context, our synthesis validates past studies that reported the distinct yet partially complementary roles of the DAN and the VAN, underscoring their interplay in flexible attentional control (Vossel et al., 2014). Furthermore, modulations at the network level have direct behavioral consequences. Excitatory NIBS protocols, such as iTBS (Anderkova et al., 2018) and high-frequency tRNS (Contò et al., 2021), have been shown to enhance functional connectivity between attentional control brain regions. This improves their integration and supports task performance. Interestingly, increased connectivity has also been reported following cathodal tDCS, despite its traditionally inhibitory effects (Tsujimoto et al., 2022). This finding underscores the complexity of neuromodulatory outcomes. This paradoxical effect may reflect the interplay between stimulation parameters and the intrinsic state of the targeted networks. State dependency is now widely recognized as a key determinant of NIBS (Bradley et al., 2022). Differences in cortical excitability, oscillatory phase, or ongoing task engagement can dramatically alter whether stimulation facilitates or disrupts neural processing. For example, the differential impact of FEF stimulation on attentional shifting (Heinen et al., 2017) underscores the importance of task-specific neural recruitment in mediating the efficacy of NIBS. It is important to note that NIBS techniques differ in their interaction with brain state. Electrical stimulation methods (tDCS, tACS, and tRNS) modulate membrane potential and oscillatory activity without directly evoking action potentials. In contrast, TMS triggers localized neural firing with high spatial specificity. Notably, tRNS can modulate the signal-to-noise ratio in targeted networks, enhancing or suppressing activity depending on the baseline noise level of the network (van der Groen et al., 2022). Future research should prioritize closed-loop approaches that can adapt stimulation in real time to rapidly fluctuating neural conditions. More broadly, causal inference about attentional mechanisms will require designs that systematically manipulate both stimulation parameters and cognitive state, rather than treating state as a nuisance variable.

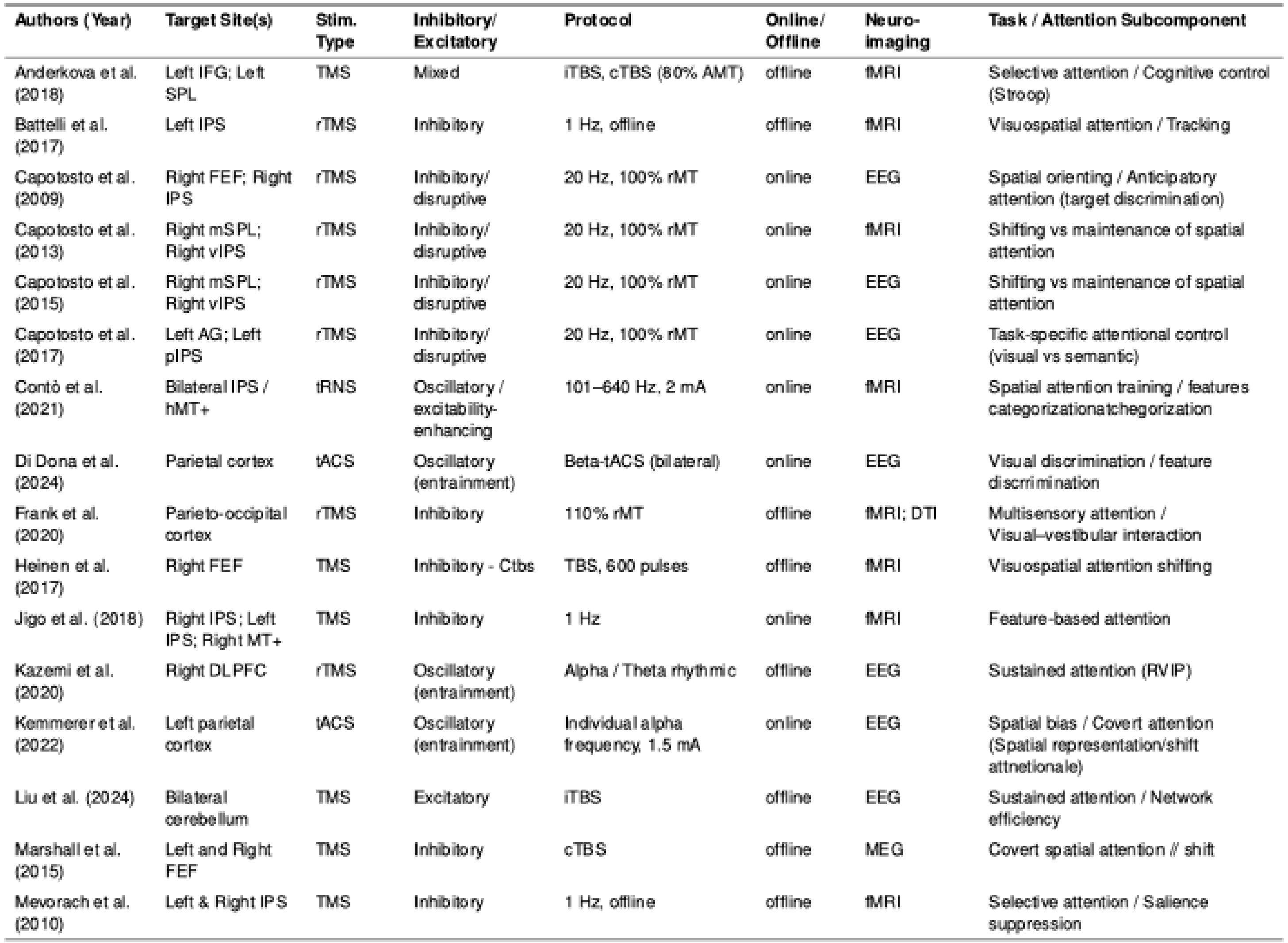
Structural variability further complicates the reproducibility of NIBS effects. Individual differences in white matter microstructure, cortical morphology, and interhemispheric connectivity influence neural responses to stimulation and attentional behavior (Harita et al., 2022; Menardi et al., 2022; Momi et al., 2021, 2023). These findings suggest a shift away from cortex-centered models and toward a more unifying neurobiological model. The integrity of the frontoparietal and callosal tracts, in particular, has emerged as a key determinant of cognitive performance (Bennett et al., 2011; Duffau, 2015; Lett et al., 2016; Yin et al., 2013), suggesting that structural metrics could serve as valuable biomarkers for predicting NIBS efficacy (Zanao et al., 2023). Integrating structural measures with functional and behavioral data is a critical step toward personalized neurostimulation and may help close the reproducibility gap in this field. The white-matter literature reviewed here also suggests that “non-responders” to stimulation may often be individuals whose structural connectivity profiles do not support efficient propagation of stimulation-induced signals, rather than evidence against the underlying mechanistic hypothesis.

Research on visuospatial attention has also been shaped by the recognition that spatial allocation is non-uniform across the visual field and is strongly lateralized. Early neuropsychological studies of patients with lesions in the right hemisphere established the right hemisphere's dominance in visuospatial attention (Aglioti et al., 1997; Baldassarre et al., 2014; Bisiach et al., 1986; Giglia et al., 2011; Nyffeler et al., 2008; Vallar & Calzolari, 2018). More recent evidence implicates interhemispheric balance as a central mechanism supporting attentional allocation (Schintu et al., 2021; Tsujimoto et al., 2022). However, contradictory results, such as the variable effects of alpha-tACS documented by van Schouwenburg et al. (2017, 2018), highlight the ongoing complexities surrounding hemispheric interactions and frequency-specific modulation. These inconsistencies likely arise from variability in methodology and inadequate control over parameters such as stimulation frequency, duration, and inter-session interval (Kemmerer et al., 2022; Radecke et al., 2023). Systematic, parameter-sensitive designs are needed to clarify the conditions under which frequency-targeted stimulation reliably influences attentional lateralization. In this sense, oscillation-based interventions provide a stringent test case for the broader field: even rhythmically aligned, anatomically plausible protocols yield mixed results, which underscores the necessity of integrating individualized structural and state information into future designs.

In summary, integrating NIBS and neuroimaging has significantly advanced our understanding of visuospatial attention by providing causal evidence of the link between network dynamics and behavior. However, the field is still marked by heterogeneous methodological approaches, unresolved questions about state- and structure-dependent variability, and conflicting findings about lateralization effects. Addressing these challenges requires more rigorous standardization of stimulation protocols, systematic manipulation of stimulation parameters, and adoption of real-time, adaptive, and multimodal approaches. Only through such methodological refinement can the field progress toward mechanistically grounded, reproducible insights into attentional control, which will ultimately enable the translation of experimental findings into individualized therapeutic interventions. Crucially, future progress will depend on treating attention not as a monolithic construct, but as a set of interacting subprocesses implemented by partially overlapping networks whose causal contributions can only be understood in the context of the structural and state-dependent constraints reviewed here.

Finally, future research should prioritize methodological innovations that address the key sources of variability that currently limit the reproducibility and translational impact of NIBS in visuospatial attention. Closed-loop stimulation paradigms, which adapt parameters in real time to ongoing neural states, show great promise in enhancing the specificity and reliability of network-level modulation. Combining these approaches with multimodal neuroimaging is essential to disentangling the causal dynamics between attentional subcomponents and their supporting neural circuits. Additionally, integrating structural biomarkers, such as white matter integrity and network connectivity, into experimental designs could enable individualized parameter optimization and improved prediction of stimulation outcomes. Addressing the heterogeneity of attentional constructs requires systematically testing stimulation effects across tasks that isolate sustained, selective, feature-based, spatial, and attentional shifting attention, while maintaining methodological consistency. Finally, future studies should explore how to translate these mechanistic insights into clinical contexts, particularly for disorders characterized by attentional deficits. This can be achieved through rigorous trials that leverage personalized stimulation protocols to maximize therapeutic benefit.

Table 1. Overview of non-invasive brain stimulation (NIBS) studies investigating attention subcomponents.



Authors (Year)	Target Site(s)	Stim. Type	Inhibitory/ Excitatory	Protocol	Online/ Offline	Neuro-imaging	Task / Attention Subcomponent
Anderkova et al. (2018)	Left IFG; Left SPL	TMS	Mixed	iTBS, cTBS (80% AMT)	offline	fMRI	Selective attention / Cognitive control (Stroop)
Battelli et al. (2017)	Left IPS	rTMS	Inhibitory	1 Hz, offline	offline	fMRI	Visuospatial attention / Tracking
Capotosto et al. (2009)	Right FEF; Right IPS	rTMS	Inhibitory/ disruptive	20 Hz, 100% rMT	online	EEG	Spatial orienting / Anticipatory attention (target discrimination)
Capotosto et al. (2013)	Right mSPL; Right vIPS	rTMS	Inhibitory/ disruptive	20 Hz, 100% rMT	online	fMRI	Shifting vs maintenance of spatial attention
Capotosto et al. (2015)	Right mSPL; Right vIPS	rTMS	Inhibitory/ disruptive	20 Hz, 100% rMT	online	EEG	Shifting vs maintenance of spatial attention
Capotosto et al. (2017)	Left AG; Left pIPS	rTMS	Inhibitory/ disruptive	20 Hz, 100% rMT	online	EEG	Task-specific attentional control (visual vs semantic)
Contò et al. (2021)	Bilateral IPS / hMT+	tRNS	Oscillatory / excitability-enhancing	101–640 Hz, 2 mA	online	fMRI	Spatial attention training / features categorizationatchegorization
Di Dona et al. (2024)	Parietal cortex	tACS	Oscillatory (entrainment)	Beta-tACS (bilateral)	online	EEG	Visual discrimination / feature discrrimination
Frank et al. (2020)	Parieto-occipital cortex	rTMS	Inhibitory	110% rMT	offline	fMRI; DTI	Multisensory attention / Visual–vestibular interaction
Heinen et al. (2017)	Right FEF	TMS	Inhibitory - Ctbs	TBS, 600 pulses	offline	fMRI	Visuospatial attention shifting
Jigo et al. (2018)	Right IPS; Left IPS; Right MT+	TMS	Inhibitory	1 Hz	online	fMRI	Feature-based attention
Kazemi et al. (2020)	Right DLPFC	rTMS	Oscillatory (entrainment)	Alpha / Theta rhythmic	offline	EEG	Sustained attention (RVIP)
Kemmerer et al. (2022)	Left parietal cortex	tACS	Oscillatory (entrainment)	Individual alpha frequency, 1.5 mA	online	EEG	Spatial bias / Covert attention (Spatial representation/shift attnetionale)
Liu et al. (2024)	Bilateral cerebellum	TMS	Excitatory	iTBS	offline	EEG	Sustained attention / Network efficiency
Marshall et al. (2015)	Left and Right FEF	TMS	Inhibitory	cTBS	offline	MEG	Covert spatial attention // shift
Mevorach et al. (2010)	Left & Right IPS	TMS	Inhibitory	1 Hz, offline	offline	fMRI	Selective attention / Salience suppression

Authors (Year)	Target Site(s)	Stim. Type	Inhibitory/ Excitatory	Protocol	Online/ Offline	Neuro-imaging	Task / Attention Subcomponent
Painter et al. (2015)	Right MT+; Right TPJ	TMS	Excitatory	Standard iTBS	offline	EEG	Feature-based attention / Attentional capture
Plow et al. (2014)	Left IPS	rTMS	Inhibitory	1 Hz, offline	offline	fMRI	Visuospatial tracking/Sustained Attention
Quentin et al. (2013)	Right FEF	TMS	Inhibitory	Single-pulse	online	MRI (DTI)	Visual detection - features categorizationatchegorization
Quentin et al. (2016)	Right FEF	rTMS	Oscillatory / excitatory-biased	30 Hz rhythmic	online	MRI (DWI)	Visual contrast sensitivity // features discrimination
Radecke et al. (2023)	Left & Right PPC	tACS	Oscillatory (entrainment)	Parietal alpha-tACS	online	EEG	Covert spatial attention / shift feature disctiminatin
Ramírez-Guerrero et al. (2025)	Right IPL	TMS	Perturbational	Train of three or six pulses	online	MRI; DWI; NODDI	Endogenous vs exogenous orienting
Rostami et al. (2021)	mPFC	tACS	Oscillatory (entrainment)	6 Hz, 1.5 mA	offline	EEG	Sustained attention
Schintu et al. (2021)	Right PPC	rTMS	Inhibitory	cTBS	offline	fMRI; DTI	Spatial bias / Pseudoneglect
Song et al. (2019)	Left & Right MFG	TMS	Inhibitory	Single-pulse	online	EEG	Sustained vs selective attention
Tsujimoto et al., 2022	PPC	tDCS	Mixed	Right cathodal and left anodal tDCS	offline	fmri	Spatial Representation/Visual Search/Shift/
van Schouwenburg et al. (2017)	Right frontal & parietal cortex	tACS	Oscillatory (connectivity modulation)	Alpha, in-phase	online	EEG	Spatial attention bias
van Schouwenburg et al. (2018)	Right frontal & parietal cortex	tACS	Oscillatory (connectivity modulation)	Alpha, in-phase vs anti-phase	online	EEG	Spatial attention bias
Williams et al. (2024)	Left or Right IPL	rTMS	Inhibitory	cTBS; 600 trains	offline	fMRI	State-dependent attentional control/
Wu et al. (2015)	Right TPJ	tDCS	Mixed	Anodal / Cathodal / Sham	offline	fMRI	Top-down vs bottom-up integration/ feature cathegorization
Zhang et al. (2022)	Left DLPFC	tDCS	Excitatory	Anodal vs Sham	offline	rs-fMRI	Distractor suppression/selective attention

3. CHAPTER 3: Hemispheric Dissociation Revealed by Attentional Isolation and tRNS

3.1. Abstract

Prolonged cognitive imbalance, induced by directing attention to one visual field, can paradoxically enhance performance in the opposite, non-attended visual field. This effect is likely driven by the brain's homeostatic mechanisms that regulate excitation and inhibition between hemispheres in homotopic attention processing regions. Here, we employed tRNS to modulate cortical excitability and probe its role in interhemispheric dynamics controlling visual attention. Specifically, we used a procedure called attentional isolation, where neurotypical participants covertly focused their visual attention in one hemifield (the attended visual field) for 30 minutes. Performance changes in both the unattended (opposite) visual field and the attended visual field were measured following this manipulation. We applied tRNS over the right or left frontoparietal cortex to modulate the excitability of one hemisphere relative to the other during attention isolation, probing the neural mechanisms underlying the observed contralateral performance shift. Our results showed improved performance in the previously unattended visual field following the attentional isolation period after sham stimulation. However, tRNS revealed a functional dissociation between the hemispheres: right hemisphere active stimulation abolished the performance improvement, while left hemisphere stimulation preserved it. These findings suggest distinct roles for the left and right hemispheres in modulating paradoxical visual performance shifts and may inform the development of novel neurorehabilitation strategies for clinical populations.

3.2. Introduction

To prevent cognitive saturation, the brain must continuously select behaviorally relevant inputs while suppressing irrelevant ones—a process governed by selective attention (Carrasco, 2011; Kastner & Buschman, 2017; Kastner & Ungerleider, 2000). This function is supported by the DAN, a system critical for endogenous, goal-directed attention (Corbetta & Shulman, 2002), whose connectivity strength correlates with visuospatial task performance (Contò et al., 2021).

Balanced attentional function depends on transcallosal communication between homotopic cortical regions, mediated by excitatory and inhibitory interactions (Bertolucci et al., 2018; Palmer et al., 2012; Tatti et al., 2017). Although these connections are primarily excitatory, inhibitory mechanisms can emerge during simultaneous bilateral activity (Palmer et al., 2012). Mutual inhibition plays a key role in shaping hemispheric contributions to attention, and its disruption — especially after parietal stroke — can cause hemispatial neglect, characterized by deficits in attending to the contralesional visual field (Casula et al., 2021; Cazzoli et al., 2010; Cazzoli, Müri, et al., 2009; Corbetta et al., 2005). The severity of neglect correlates with the extent of E/I imbalance (Baldassarre et al., 2014), which can be targeted therapeutically with noninvasive brain stimulation (Baldassarre et al., 2014; Giglia et al., 2011; Smit et al., 2015).

Transcranial random noise stimulation is a noninvasive technique that modulates cortical excitability and functional connectivity (Contò et al., 2021; Herpich et al., 2018). It has shown promise across domains, including visuospatial (Contò et al., 2023), visuoperceptual (Herpich et al., 2018), motor (Moret et al., 2019; Ellena et al., 2025), and auditory (Van Doren et al., 2014) processing. Though its mechanisms are not fully known, tRNS may enhance signal-to-noise ratio, facilitating plasticity (Antal & Herrmann, 2016; Fertonani et al., 2011; Potok et al., 2022).

Studies on homeostatic plasticity suggest that sensory imbalance can induce compensatory changes in cortical excitability. For example, unilateral handgrip training can improve function in the non-trained hand via cross-education (Andrushko et al., 2023; Ehrensberger et al., 2016). In the visual domain, temporary deprivation enhances responsiveness in the deprived eye, mediated by GABAergic modulation (Binda et al., 2018; Frangou et al., 2019; Lunghi, Berchicci, et al., 2015; Wenner, 2011).

Building on these insights, we investigated interhemispheric mechanisms in attentional control using attentional isolation, a behavioral paradigm shown to improve performance in the previously unattended hemifield (Edwards et al., 2021). We combined this with tRNS over the left or right frontoparietal cortex (targeting FEF and IPS) to examine how stimulation alters the plasticity induced by unbalanced attention deployment.

Given the right hemisphere's dominant, bilateral role in visuospatial attention (Bartolomeo & Seidel Malkinson, 2019; Brancaccio et al., 2022), we hypothesized that tRNS over the right frontoparietal cortex would interfere with homeostatic rebalancing. In contrast, left hemisphere stimulation is more specialized for contralateral attention and was expected to preserve or enhance the behavioral effect. This design allowed us to test whether tRNS modulates interhemispheric attentional control and to explore its implications for neurorehabilitation.

3.3. Experiment 1 – Unilateral *right* stimulation

3.3.1. Methods

3.3.1.1. Participants

Forty-five neurologically healthy (mean age 24.83, SD 3.84, 26 female), right-handed individuals, with normal or corrected-to-normal vision, were enrolled in this study. All subjects met all brain stimulation screening criteria (Fried et al., 2021) and provided informed consent approved by the ethics committee of the University of Trento. The study conformed to the Declaration of Helsinki. Subjects received monetary compensation for their participation in the study. Six subjects after the first session were excluded from the experiment due to poor compliance with the study design, leaving a total of 39 subjects. Poor compliance was primarily attributed to difficulties in adjusting to the eye-tracking acquisition and maintaining central fixation for a prolonged period of time.

3.3.1.2. Bilateral multiple object tracking

Participants performed a bilateral MOT task, which required participants to track two moving disks in each hemifield among distractors. In each trial, four disks were displayed in each hemifield within a 6 cm by 6 cm area (four disks on the right hemifield and four disks in the left hemifield). All disks were black (Figure 11B), with a radius of 0.25cm. Each disk could never cross the midline and repelled the others to avoid collisions. Two disks on each side of the fixation briefly flashed at 4 Hz, indicating the target disks to track during each trial. Importantly, the selection of target disks was random, and participants could not predict in which visual field they would be tested. Following the flashing cues, all the disks moved at a constant speed for a duration of 2 seconds. The individual speed threshold for each participant was measured at baseline using a staircase procedure (see the "Thresholding MOT" section for details). At the end of the 2-second movement period, all disks stopped, one disk turned red, and subjects were asked to indicate whether it was a target or a distractor by entering their response on a keyboard. The target could appear randomly in the right or left visual field. Response feedback was provided, with the fixation point turning green for correct and red for incorrect responses. Throughout the task, participants were instructed to maintain their gaze on the fixation, monitored with an eye tracker (see "Eye-tracking acquisition" section for details). When they broke the fixation, the trial was aborted, and a new trial began. On average, participants performed 106 trials on pre-test (SD = 6.61), 309 on attentional isolation (SD=25.45), and 107 on *post*-test (SD=6.23). During the 30 minutes of attentional isolation, on average, subjects performed 103 trials (SD=9.58) every 10 minutes. Participants were tested on a Samsung 2233RZ LCD (22") monitor (screen resolution 1680x1050), at a distance of 70 cm. The experiment was run through a 2020 HP Pavilion Gaming Laptop (Windows 10 installed). The stimuli were presented using the psychophysical toolbox PsychoPy 2022.2.0.

3.3.1.3. Study design

Experimental design is briefly summarized in Figure 11A. Subjects were randomly assigned to three different manipulation groups: Group 1 performed a right unilateral MOT, Group 2 performed a left unilateral MOT, and Group 3 underwent a bilateral MOT task (Figure 11C). The manipulation time lasted 30 minutes for each session. During unilateral MOT, participants were instructed to track two moving target disks among two moving distractor disks presented in one hemifield (a total of 4 disks). Four additional moving disks were simultaneously displayed in the contralateral hemifield to maintain a homogeneous sensory input between the two hemifields. During the bilateral MOT control condition, participants were asked to simultaneously track four target disks (two in each hemifield) among four distractor disks (two in each hemifield). Participants were required to focus on the attended hemifield while actively ignoring the unattended contralateral hemifield. The task was gaze-contingent (see section *Eye-tracking acquisition), and when subjects broke fixation,* the trial was aborted, and a new trial started. The sample size of the study was based on the previous work of Edwards et al. (2021).

All Subjects (Groups 1, 2, and 3) underwent two counterbalanced sessions: a sham and an active stimulation condition separated by at least seven days. In Experiment 1, 39 subjects received stimulation over the right hemisphere. While in Experiment 2, 26 subjects received stimulation over the left hemisphere. Based on previous literature (Edwards et al., 2021) and on the results of Experiment 1, we decided not to include a bilateral MOT condition in Experiment 2, since we already expected no effect on this control condition. For both experiments, 13 subjects were assigned to each group.

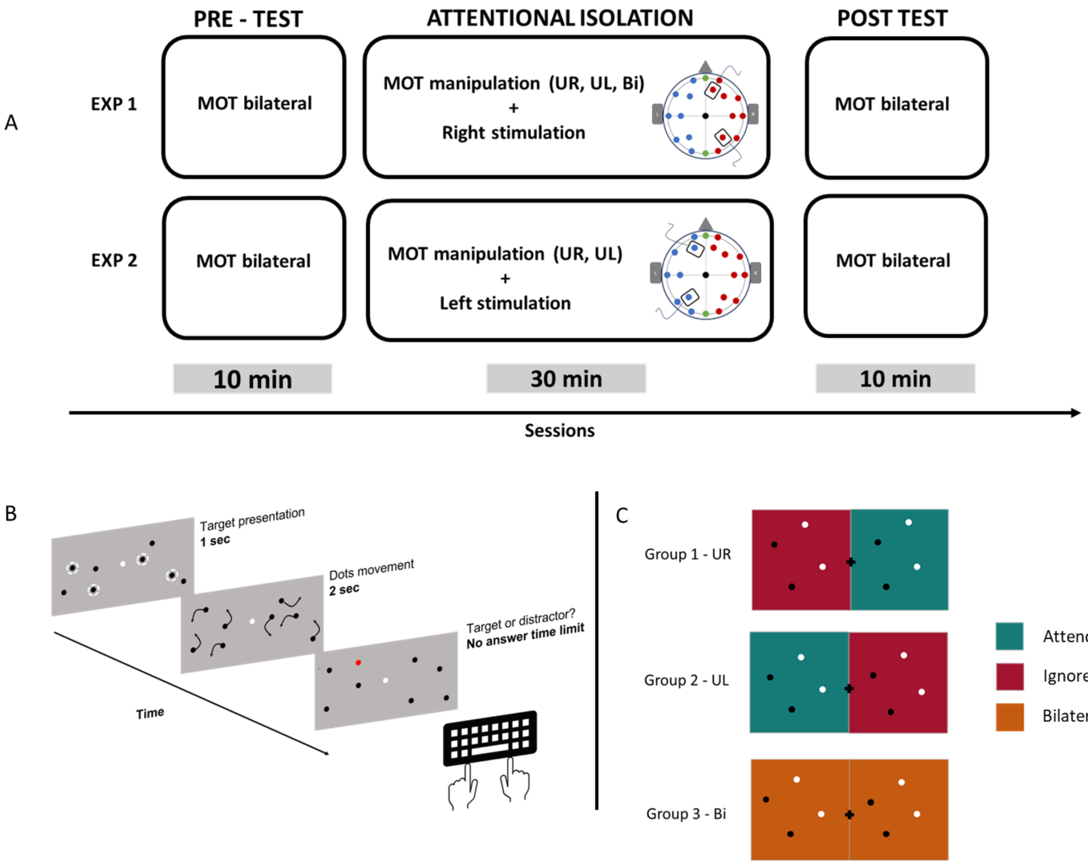


Figure 11 *– Procedure and stimulation locations.* ***(A)*** *At the beginning of the experiment, threshold and pre-test performance were assessed. Subjects were then assigned to a specific "isolation group" (UL - unilateral left, UR - unilateral right, Bi - bilateral control). The attentional isolation lasted 30 minutes. Simultaneously, from the beginning of the attentional isolation, subjects received 20 minutes of tRNS at 2mA. After the manipulation, subjects immediately underwent a bilateral post-test and a retest 10 minutes after the end of the post-test.* ***(B)*** *MOT design - This task involved identifying and tracking specific objects (two moving disks) among a group of distractor disks.* ***(C)*** *Hemifield tracked during the 30 minutes of attentional isolation for each group. Each color represents one tracking condition.*

3.3.1.4. Thresholding MOT

At the beginning of each experimental session, we psychophysically measured participants' speed threshold in the MOT task. A 2AFC with fixed step sizes staircase was employed to determine the speed at which subjects performed at 70% correct. We used a staircase procedure to adjust the stimulus motion speed based on participants' performance: it increased by 0.5 cm/sec after two correct consecutive responses and decreased after one single incorrect response. The staircase procedure continued until it reached a predefined endpoint of 20 reversals. Importantly, only the data from the last six reversals were used to estimate individual accuracy performance, ensuring a stable and reliable measure of participants' tracking abilities before the experimental manipulation. Prior to the thresholding, subjects practiced bilateral MOT for 120 sec, at a fixed speed of 3.5 cm/s. On average, participants performed the MOT after the threshold with a mean speed of 8.17 cm/sec, std 2.56 cm/sec, ranging from 2.5 cm/sec to 15.17 cm/sec.

3.3.1.5. Eye-tracking acquisition

Central fixation was continuously monitored with an EyeLink 1000 Plus eye-tracking system (SR Research). Calibration and validation were performed at the beginning of each run. Throughout the experiment, a box of 3° × 3° was placed around the central fixation point. If participants shifted their gaze outside of this boundary box, the trial would restart.

3.3.1.6. Stimulation protocol

A battery-powered device (DC-Stimulator, manufactured by NeuroConn in Ilmenau, Germany) was used to deliver the electrical stimulation. In the absence of neuronavigation, electrode positions were estimated using anatomical landmarks. Electrodes, each measuring 5×5 cm^2 and inserted in sponges soaked with saline solution, were positioned according to the 10/20 International System (Herwig et al., 2003; Okamoto et al., 2004), over F2 and P4 for the right hemisphere and F1 and P3 for the left hemisphere, roughly corresponding to the FEF and the IPS, in each hemisphere. In Experiment 1, electrodes were placed over the right hemisphere, while in Experiment 2, over the left hemisphere. The stimulation was administered for the first 20 minutes within the period of isolation, with a current intensity of 2mA peak-to-peak at a high frequency range, ranging randomly from 101 to 640 Hz. A gradual fade-in/fade-out period lasting 10 sec preceded and followed the stimulation. In the sham condition, the stimulation ceased after 30 seconds plus the fade-in/fade-out period. Importantly, participants did not report any significant adverse effects following the stimulation.

3.3.1.7. Data analysis

Statistical analyses were conducted in RStudio, using the *tidyverse* and *lme4* packages (Bates et al., 2014; Wickham et al., 2019). Figures were made in the R package *ggplot2* (Wickham, 2016). We first checked if the pre-test baseline performance was equal across groups. Pre-test performances were tested with a specific *glmer* from the *lme4* package. Effect sizes were computed as odds ratios (*glmer*) and Cohen's d (*lmer*). The between-subjects predictors were Manipulation (attended visual field, ignored visual field, or control) and Montage (right montage, left montage); the within-subjects predictors were visual field (left, right), stimulation (sham, active), and Session (Pre, Post). Outliers within the visual field for each experiment at baseline were removed with the interquartile range method. Specifically, average individual performance values that surpassed the upper quartile plus 1.5 times the interquartile range (IQR) or fell below the lower quartile minus 1.5 times the IQR were identified as outliers and removed from the analysis. A simulation-based power analysis conducted with G*Power 3.1 indicated that a minimum sample size of 30 participants would be required in Experiment 1 to achieve 80% statistical power at a significance level of $\alpha = 0.05$, assuming a small-to-medium effect size ($f = 0.25$) - (Lakens, 2013). An analysis to detect changes in performance from pre to during to post was run using a *glmer* model. Post-hoc comparisons were performed using the emmeans package (Lenth, R 2024) and the Holm correction. Finally, the comparison of gain in performance (delta, calculated as post - pre) was performed using an *lmer*.

3.3.2. Results

3.3.2.1. Isolation manipulation impact on tracking performance.

We first checked for outliers in the pre-test conditions, and we did not find any for either the *left* or *right* visual field. Importantly, we did not find any *pre*-test baseline difference in performance between manipulation conditions ($\chi2(2) = 0.30$, $p = 0.85$, $N = 39$, *glmer*) and stimulation conditions ($\chi2(1) = 0.64$, $p = 0.42$, $N = 39$, *glmer*). First, we investigated the impact of isolation manipulation on tracking accuracy (attentional gain) in the ignored visual field relative to the (bilateral tracking) control condition. We expected an increase in tracking accuracy in the ignored visual field after the manipulation period, and no significant changes from pre to post in the attended visual field and in the bilateral tracking condition. We then examined the effect of right frontoparietal stimulation on attentional gain following the manipulation period. We found a three-way interaction between manipulation, session, and stimulation, suggesting that the effect of the manipulation changed across sessions and between stimulation conditions ($\chi2(2) = 6.69$, $p < .05$, N =39, *glmer*). A post-hoc comparison revealed a change from pre- to post-manipulation in the ignored visual field in the sham condition (estimate = 0.48, se= 0.08, z=5.45, $p < .01$, OR = 1.63, 95 % CI [1.20, 2.20], Figure 12 - sham), while we did not find any change in performance between the pre- and post-manipulation in the ignored visual field in the active stimulation condition (estimate = -0.05, se=0.08, z=-0.67, $p > .05$, OR = 0.94, 95 % CI [0.71, 1.25], Figure 12 - active). Therefore, attentional isolation resulted in a significant increase in tracking accuracy in the ignored visual field during sham. However, the significant gain in accuracy was abolished after right frontoparietal stimulation. Importantly, to see whether unilateral tRNS had any effect in the absence of any attentional manipulation, we also compared performance in the left hemifield, contralateral to the stimulation, in the bilateral control group for sham versus active stimulation. We found no change in response between active and sham ($\chi2(1) = 0.28$, p = 0.59, N = 13, *glmer*), indicating that tRNS had a significant impact only during the attentional manipulation.

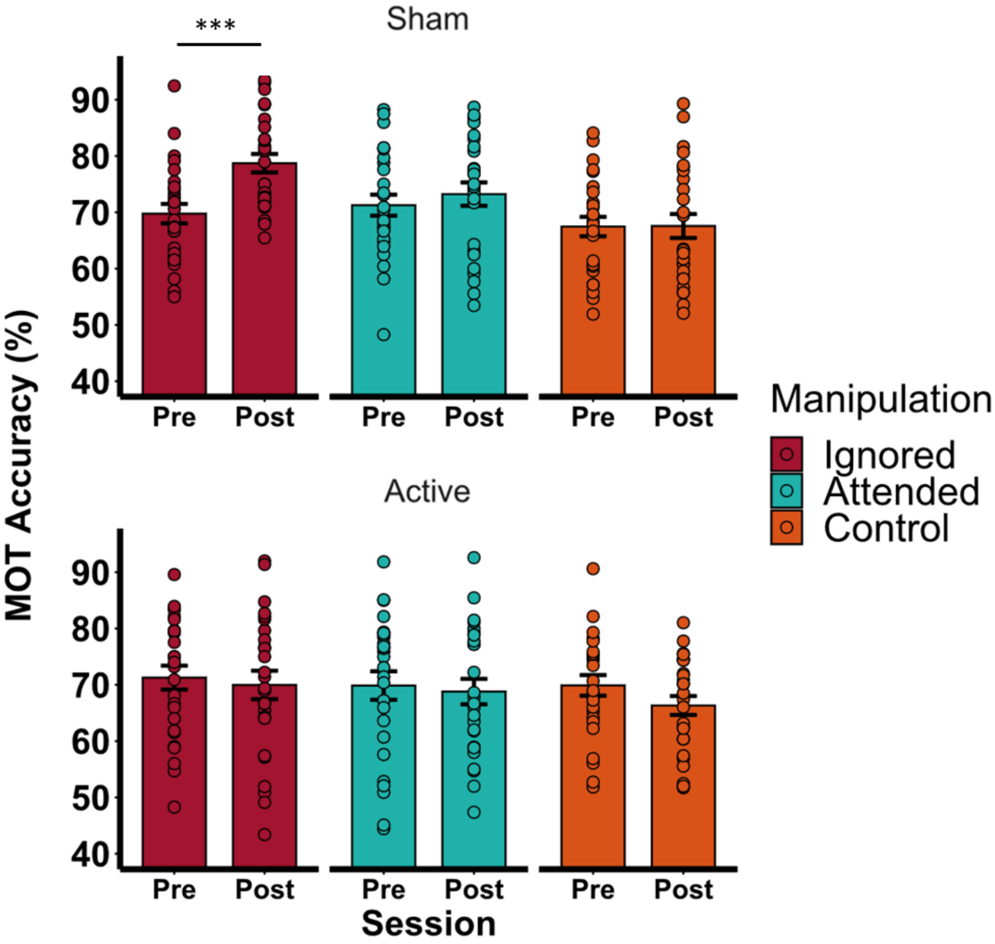


***Figure 12** – Change in accuracy from Pre to Post over different Manipulation conditions (Ignored hemifield, Attended hemifield, Control), for the Sham (top graph) and Active (bottom graph) stimulation for the right montage condition.*

3.4. Experiment 2 – Unilateral *left* stimulation

3.4.1. Methods

The procedure was kept identical to Experiment 1, except for the stimulation site. We also did not include a bilateral tracking control group, as we already replicated the effect we found in our previous study, and to increase the statistical power (Edwards et al., 2021). We used the same electrode montage as in Experiment 1, but for *left* FEF-IPS (corresponding to electrodes F1-P3) in accordance with the 10-20 international EEG system. Twenty-nine neurologically healthy (mean 22.27, std 2.65, 19 female) right-handed individuals, with normal or corrected-to-normal vision, were enrolled in this study. Three subjects were excluded from the experiment after the first session due to poor compliance with the study design, leaving 26 subjects. All subjects met all brain stimulation screening criteria (Fried et al., 2021) and provided informed consent approved by the ethics committee of the University of Trento. The study conformed to the Declaration of Helsinki. Subjects received monetary compensation for their participation in the study. For Experiment 2, simulation-based power analyses showed that a sample size of 24 participants yields approximately 81% power at $\alpha = 0.05$ for the same expected effect size (f = 0.25).

3.4.2. Results

3.4.2.1. Isolation manipulation impact on tracking performance

We first checked for outliers in the pre-test conditions for all subjects. After the outlier detection, four subjects were removed from the sample. Importantly, we did not report any pre-test differences between manipulation conditions ($\chi2(1) = 2.33$, $p = 0.12$, $n = 22$, *glmer*), nor between stimulation conditions ($\chi2(1) = 0.41$, $p = 0.51$, $n = 22$, *glmer*). Similar to experiment 1, we were interested in investigating the effect of a prolonged unilateral tracking period on the contralateral, ignored portion of the visual field. Furthermore, we expected left frontoparietal tRNS to have a weaker impact on performance compared to right frontoparietal stimulation. As previously reported, we expected an improvement in the ignored visual field compared to the pre-test. We did not find a three-way interaction between session, manipulation, and stimulation ($\chi2(1) = 0.001$, $p>.05$, $n = 22$, *glmer*). However, we found a two-way interaction between session and manipulation, suggesting that the effect of attentional isolation changed across time, independently from the stimulation ($\chi2(1) = 11.18$, $p <. 01$, $n = 22$, *glmer*). Post hoc analysis revealed a change in tracking accuracy from pre- to post-manipulation in the ignored visual field (estimate=0.26, se=0.06, z=4.04, $p < .01$, OR = 1.29, 95 % CI [1.10, 1.54]; Figure 13), indicating a gain in performance over the ignored visual field. We also reported a change in performance from pre to post in the attended visual field (estimate = -0.17, se=0.06, z=-2.68, p < .05*;* OR = 0.84, 95 % CI [0.71, 0.99]; Figure 13), revealing a detrimental effect on tracking accuracy over the attended visual field after the attentional isolation.

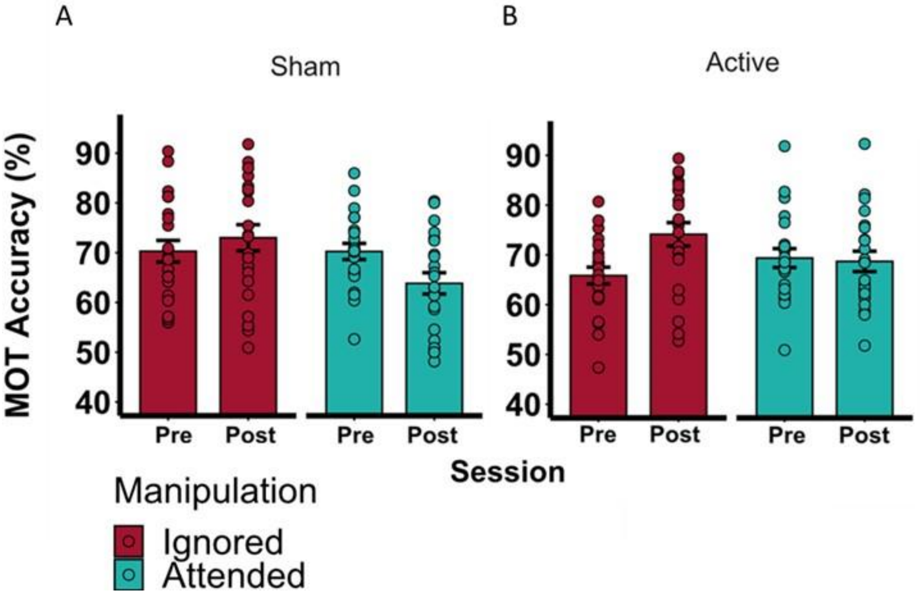


Figure 13 *– Change in accuracy from pre- to post-manipulation for the Sham (A) and for the Active (B) stimulation condition, for the Ignored (red) and the Attended (green) visual hemifield for the Left Montage stimulation condition. In our model, Sham and Active did not report any statistical differences.*

3.4.2.2. Comparison between left and right hemisphere stimulation in the ignored visual field

Based on the results of Experiments 1 and 2, we decided to further analyze the changes in pre- versus post-stimulation performance between left and right stimulation in both experiments over the *ignored visual field*. We found a two-way interaction between montage and stimulation, indicating that the effects induced by stimulation varied between right and left montages ($\chi 2(1) = 16.40$, $p < .01$, n = 48, lmer). As expected, we found a change in accuracy from pre- to post-manipulation (delta) in the ignored visual fields between the right and left (active) stimulation conditions (estimate= -0.09, se=0.03, t=-3.18, p < .05), indicating that the magnitude of attentional enhancement over the ignored visual field is different following left and right hemisphere stimulation, thus highlighting a dissociation in the stimulation effects between the left and right hemispheres (Figure 14). The associated Cohen's d value was -1.005 (95% CI: -1.65, -0.36). Finally, we found no differences in the magnitude of attentional enhancement in the ignored visual field in the sham condition in both Experiments 1 and 2.

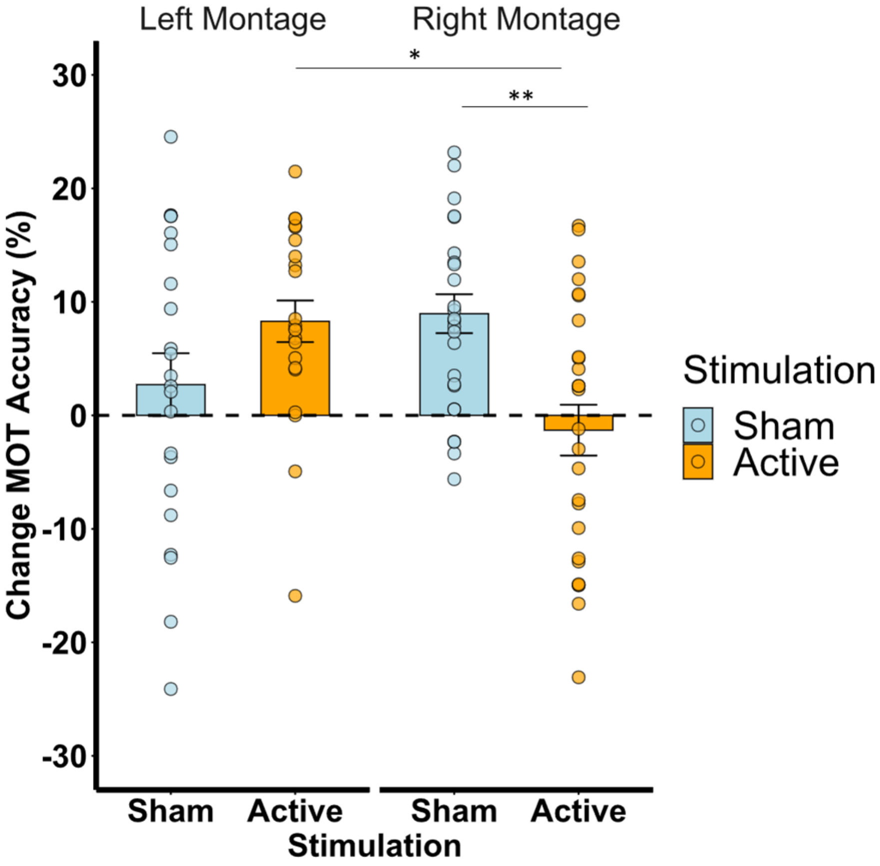


Figure 14 *– Changes in performance pre- versus post–stimulation for the right and left montage in the Ignored Visual Field.*

3.4.2.3. Hemispheric-dependent response to tRNS during the attentional isolation

We conducted additional analyses to examine the effect of attentional isolation in the attended visual field to test for hemispheric asymmetries during the manipulation. Given that the beneficial post-manipulation effect was present after the left frontoparietal tRNS but was abolished after the right tRNS, we sought to better understand the dynamics of the cortical response to stimulation during the manipulation in the attended visual fields (isolation side). Specifically, we ran a model to examine changes in performance over the isolation side (ipsilateral or contralateral to the stimulation site) during the 30 minutes of attentional isolation in the active condition relative to sham for both hemispheres (left and right montage). We found a three-way interaction between stimulation, montage, and side of isolation ($\chi2(1) = 26.57$, $p <.01$, $n = 48$, *glmer*), suggesting that the effect of the stimulation (sham or active) during the attentional isolation manipulation depended on montage (left or right hemisphere) and the attended side (ipsilateral or contralateral to stimulation). Right stimulation during attentional isolation had a detrimental effect for both the ipsilateral and contralateral sides (Figure 15, right montage). Specifically post-hoc analysis revealed that there was a decrease in tracking accuracy during right hemisphere stimulation relative to sham in the (attended) contralateral side (estimate = -0.23, se =0.05, z = -3.90, p < .01, OR = 0.79, 95 % CI [0.66, 0.95]) and during right hemisphere stimulation relative to sham on the (attended) ipsilateral side (estimate =-0.36, se =0.05, z = -6.45, p < .01, OR = 0.69, 95 % CI [0.57, 0.82]). This suggests that performance in both hemifields was impaired by the application of tRNS over the right hemisphere at the same time as the task. In other words, the effect of stimulation during the attentional isolation manipulation was detrimental bilaterally (Figure 15). Furthermore, we observed an improvement in ipsilateral tracking accuracy during left hemisphere stimulation compared to the sham condition (estimate =0.23, se =0.05, z = 3.91, p <. 01, OR = 1.26, 95 % CI[1.04, 1.52]), whereas contralateral tracking accuracy decreased during left hemisphere stimulation compared to sham (estimate =-0.25, se =0.06, z = -3.70, p < .01, OR = 0.77, 95 % CI [0.62, 0.96]). Finally, we did not find an effect of the right stimulation on the bilateral control group during the attentional isolation ($\chi2(1) = 0.82$, $n = 13$, $p > .05$, *glmer*). In short, left hemisphere stimulation during task performance tends to facilitate tracking performance ipsilateral to stimulation, while contralateral tracking performance is impaired (Figure 15, left montage).

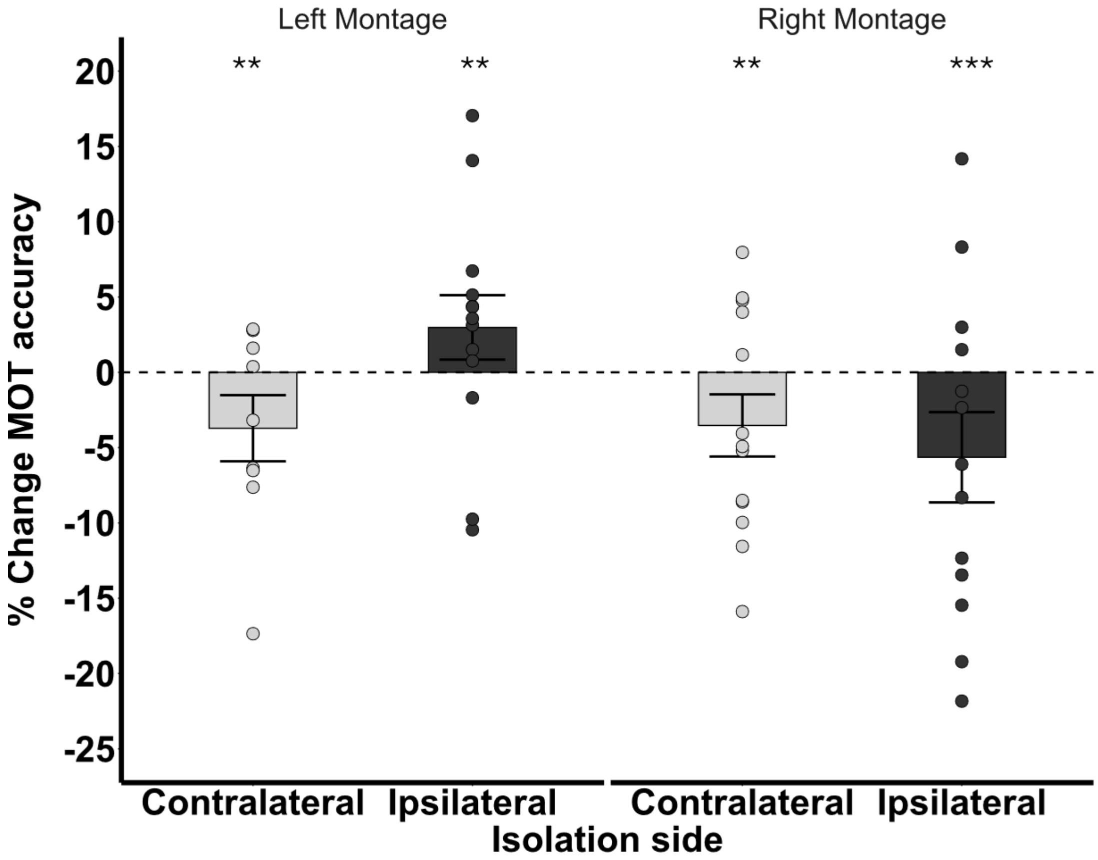


Figure 15 *- Percent change in MOT accuracy reported as the difference between Active and Sham (delta) for isolation sides and conditions.*

3.5. Discussion

Our results show a clear hemispheric asymmetry in how frontoparietal tRNS modulates attentional reallocation. Specifically, left frontoparietal tRNS preserved the post-manipulation improvement in the ignored visual field observed *after* participants performed a MOT tracking task. In contrast, right frontoparietal tRNS abolished this beneficial effect observed in previous work (Edwards et al., 2021). *During* the manipulation period, when participants were asked to focus on tracking multiple moving objects in one visual hemifield for 30 min while actively ignoring objects in the opposite, unattended field, tRNS effects were also hemisphere-specific: right hemisphere stimulation impaired performance in both visual fields, whereas left hemisphere stimulation selectively reduced performance in the contralateral visual field and improved it ipsilaterally. These effects were not present in a bilateral MOT control condition, suggesting that the effects were solely due to the combination of manipulation and stimulation. These results suggest that left frontoparietal stimulation may facilitate adaptive attentional reallocation, while right hemisphere stimulation disrupts it, likely due to differences in each hemisphere’s role in spatial attention. The beneficial behavioral effect of attentional isolation observed in the sham condition replicated earlier findings (Edwards et al., 2021), but the concurrent application of active tRNS altered this outcome. In particular, right frontoparietal tRNS eliminated the post-manipulation gain, suggesting a disruptive interaction between stimulation and endogenous attentional processes during the manipulation. Thus, our results underscore the importance of hemispheric specialization in attentional control. The right hemisphere’s dominant role in spatial attention (Corbetta & Shulman, 2002) may explain why stimulation here leads to bilateral suppression of tracking performance (Hilgetag et al., 2001; Szczepanski & Kastner, 2013). In contrast, left hemisphere stimulation produced more localized, contralateral effects (Figure 15), consistent with prior reports (Battelli et al., 2009, 2017). These findings align with the broader literature on hemispheric asymmetries: the right hemisphere exerts bilateral attentional control, while the left hemisphere shows a stronger contralateral bias (Heilman & Van Den Abell, 1980). Furthermore, tRNS likely impacts the dorsal attention network, altering how attentional signals are integrated across hemispheres. Given tRNS’s effects on cortical excitability and connectivity (Contò et al., 2021; Moret et al., 2019), the observed behavioral changes suggest that these network-level modulations are sensitive to both the site of stimulation and the attended visual field. Taken together, these findings indicate that unilateral tRNS may suppress attentional deployment across both fields during attentional isolation, particularly when targeting the right hemisphere, while left hemisphere stimulation can have facilitatory effects in the ipsilateral field (see Figure 15). This supports neuropsychological models of interhemispheric competition and attentional vectors (Bisiach et al., 1986; Buxbaum et al., 2004; Corbetta, 2014; Kinsbourne, 1987; Mesulam, 1981; Vallar, 2001; Vallar et al., 2014; Veronelli & Vallar, 2025). In our study, right hemisphere tRNS during the manipulation may have induced inhibitory effects that disrupted attentional deployment bilaterally—consistent with its broad attentional influence (Shulman et al., 2010). Conversely, left tRNS impaired contralateral field tracking but improved performance in the ipsilateral field, likely due to a combination of lateralized attentional vectors and compensatory mechanisms from the dominant right hemisphere. This may explain why, in Experiment 2 (left stimulation), we observed preserved post-manipulation benefits, while in Experiment 1 (right stimulation), performance returned to baseline with no gain (Edwards et al., 2021). From a clinical perspective, these hemispheric effects have potential implications. Frontoparietal stimulation's impact on attentional asymmetries could inform neuromodulation strategies for patients with conditions such as hemispatial neglect (Agosta et al., 2014). Tailoring stimulation protocols based on hemispheric roles may enhance rehabilitation outcomes, and these principles could extend to other attention-related disorders (Agosta et al., 2014). The dominant role of the right parietal cortex in neglect is well-established (Bartolomeo & Chokron, 1999; Bartolomeo & Seidel Malkinson, 2019) and Kinsbourne's interhemispheric competition theory provides a useful framework: both hemispheres direct contralateral attention and inhibit each other, with the left hemisphere biasing rightward attention. Damage to the right hemisphere—or its suppression via noninvasive brain stimulation—can result in reduced attentional deployment to the left field (Kinsbourne, 1987). Lateralized effects of tRNS observed here likely reflect distinct roles of the left and right frontoparietal networks. The right IPS and FEF are involved in global attention allocation and distractor suppression, critical in our task (Szczepanski & Kastner, 2013; Corbetta & Shulman, 2002). Disrupting this network with right tRNS likely reduced attentional capacity bilaterally during the manipulation, thus abolishing the post-manipulation benefit (Edwards et al., 2021). In contrast, left hemisphere stimulation selectively impaired right-field attention, perhaps due to compensation by the right hemisphere, while preserving the post-manipulation (Hilgetag et al., 2001). Dynamic tracking requires stable excitability in lateralized networks (Howe et al., 2009; Jovicich et al., 2001). Disruptions in excitability, whether through stimulation or pathology, can inhibit contralateral processing, as seen in visual and motor systems (Ikkai et al., 2016). These findings mirror homeostatic mechanisms—e.g., enhanced processing in an ignored visual field after unilateral deprivation (Binda et al., 2018; Lunghi, Emir, et al., 2015). The neurochemical basis of tRNS, particularly its effects on GABA and glutamate balance, may help explain the observed hemispheric differences, as previously studied with noninvasive brain stimulation (Matsuta et al., 2022; Müller-Dahlhaus & Vlachos, 2013; Rodger & Sherrard, 2015; Stagg et al., 2009). An interesting question arises from our findings: while the present study shows that unilateral tRNS over (right) frontoparietal areas can have inhibitory effects, previous research suggests that bilateral tRNS over the left and right IPS can enhance visual attention learning (Contò et al., 2021). Physiological studies indicate that electrical stimulation can produce opposite effects on neural activity, even with the same stimulation protocol, depending on the cortical state at the time of stimulation (M. R. Krause et al., 2022). One hypothesis is that bilateral tRNS enhances the overall functioning of the brain's attentional network by maintaining a homeostatic balance between homologous areas in both hemispheres, thereby optimizing performance. In contrast, unilateral tRNS may disrupt this balance and prevent facilitation. However, this hypothesis remains to be empirically tested. In conclusion, this study contributes to our understanding of hemispheric asymmetries in attentional control, showing how left and right frontoparietal tRNS differentially affect spatial attention across the visual field. These findings emphasize the importance of stimulation site, timing, and cortical state in shaping behavioral outcomes and lay the groundwork for future research and clinical translation.

4. CHAPTER 4: Disentangling Neural Mechanisms of Unilateral Attentional Isolation

4.1. Abstract

In this chapter, we present preliminary EEG evidence on the neural mechanisms underlying the attentional isolation procedure. Interhemispheric competitive dynamics play a central role in attentional orienting and allocation, and these dynamics are supported by multiple neural correlates. In the present study, participants performed a 30-minute attentional isolation procedure, in which their attention was restricted to a single hemifield. The aim was to induce an attentional benefit in a MOT task in the contralateral, previously ignored hemifield. EEG recordings were used to identify and analyze ERP components associated with early visual and attentional processing. Preliminary results suggest that attentional isolation is associated with decreased N1 negativity and improved attentional tracking performance. These results suggest that plasticity-related neural mechanisms are involved in the effects of attentional isolation.

4.2. Introduction

Attention is a multifaceted cognitive function supported by multiple interacting mechanisms (Carrasco, 2011; Hanley & Tales, 2021; Kida & Okamoto, 2023). Extensive research has examined how attentional processes operate, how they can be trained or modulated, and the neural substrates that support them (Xia et al., 2024). The integration of behavioral paradigms with electrophysiological recordings allows the investigation of brain activity with high temporal resolution, providing a powerful framework for linking cognitive processes to their neural correlates (Gruzelier, 2014; Taylor, 2018; Wischnewski et al., 2018). In the domain of visuospatial attention, specific ERPs have been reliably associated with distinct phases of attentional disengagement and deployment (Perchet et al., 2001; Qin et al., 2022; Shi et al., 2022). Furthermore, ERPs provide a valuable tool to investigate experience-dependent plastic changes in the visual and attentional domains following treatment or training (Clark et al., 2015; Luck & Hillyard, 1994; Schwent & Hillyard, 1975). As briefly mentioned before, the most commonly studied ERPs in visual attention research include the C1, P1, N1, P2, N2, and N2pc components. Each component is characterized by a specific temporal profile and latency, and has been associated with distinct stages of neural processing. The C1 component, typically peaking between 50–100 ms, reflects early visual processing and is reliably elicited by stimulus onset (Qin et al., 2022, 2023). The P1, a positive deflection occurring around 100 ms, is linked to early attentional modulation, often interpreted as reflecting the initial allocation of attentional resources. Together, these components form the C1–P1 complex (Fu et al., 2010) .

The N1 component, emerging around 150–200 ms, is associated with selective attention mechanisms, including sensory enhancement and the prioritization of attended stimuli (Eimer, 1999; Lange et al., 1999). The P2 (approximately 150–275 ms) has been related to feature detection and top-down attentional filtering (Mueller et al., 2008). The N2, peaking between 200–300 ms, is commonly linked to conflict monitoring and inhibitory control processes (Donkers & Van Boxtel, 2004; Smith et al., 2010). Finally, the N2pc, a lateralized subcomponent of the N2 observed over posterior electrodes, reflects spatially selective attention mechanisms, including target selection, attentional shift and distractor suppression during visual search (Luck, 2011). This approach has been widely used in studies of visual perception and ocular dominance. For example, short-term enhancements in visual performance have been observed after monocular deprivation (Binda et al., 2018; Sarı & Lunghi, 2023). Specifically, 150 minutes of monocular deprivation alters ocular dominance, shifting visual preference toward the deprived eye, consistent with homeostatic plasticity mechanisms. At the neural level, the C1 component increases for the deprived eye and decreases for the non-deprived eye, with similar modulations observed for the P1 and P2 components (Lunghi, Berchicci, et al., 2015). These results, particularly those related to the C1 component, indicate that monocular deprivation can modulate plasticity at early stages of visual processing, likely involving V1. These findings were further supported by subsequent correlational studies investigating changes in the BOLD signal (Binda et al., 2018).

Cognitive training procedures have also been shown to enhance the neurocognitive mechanisms involved in visual search tasks. Specifically, training is associated with changes in the N1 amplitude, suggesting an enhancement of early sensory processing. Similarly, the N2pc component shows increased amplitude following training, reflecting more efficient attentional orienting toward task-relevant stimuli (Kiss et al., 2008; Luck & Hillyard, 1994). More generally, behavioral improvements are accompanied by neurocognitive changes that facilitate early perceptual processing as well as motor response preparation and execution (Clark et al., 2015).

Interplay and homeostatic mechanisms between the two hemispheres during visuospatial processing may be fundamental for leveraging neural plasticity. Within the framework of the interhemispheric competition model, recent work has demonstrated that unilateral attentional isolation can produce beneficial effects on behavioral performance. Specifically, Edwards et al. (2021) showed that isolating attention to one hemifield (attended visual field) for 30 minutes *paradoxically* enhanced performance in the contralateral, ignored visual field. Subsequent work disentangled the relative contributions of the two hemispheres underlying this paradoxical gain (see Chapter 3). The purpose of this experiment is to investigate the neural mechanisms underlying attentional isolation and the behavioral effects that follow this procedure. As a first hypothesis, at the behavioral level, we expect an improvement in performance in the ignored visual field following the attentional isolation procedure. No changes in performance are expected in the control condition. Finally, as a second hypothesis, we expect a modulation of the amplitude of the attentional ERP components following the attentional isolation procedure.

4.3. Task and procedure

4.3.1. Participants

Thirty-seven healthy participants, all with normal or corrected-to-normal vision and right-handed, took part in the study. All individuals gave written informed consent, as approved by the Ethics Committee of the University of Trento. The study was conducted in accordance with the Declaration of Helsinki, and participants received monetary compensation for their involvement.

4.3.2. Bilateral Multiple Object Tracking

Participants completed an MOT task that required tracking targets among distractors in both visual hemifields (see Chapter 3). Each trial presented eight black disks (radius = 0.25 cm), with four disks displayed per hemifield within a 6 × 6 cm area. Between consecutive trials, a brief inter-trial interval period lasting 1.9–2.1 s was presented to the participant. This inter-trial interval introduced a subtle temporal jitter and served to reduce anticipatory responses and sensory habituation, ensuring that neural activity returned to baseline before the onset of the next stimulus. At the beginning of each trial, two disks per hemifield were cued as targets via a brief 4 Hz flicker. Target selection was randomized on each trial, preventing participants from anticipating which hemifield would be tested. Following cueing, all disks moved at a constant speed for 2 seconds. Individual motion speed thresholds were determined at baseline using a staircase procedure (See *Speed Thresholding for MOT*). Disks remained confined to their respective hemifield, never crossing the vertical midline, and repelled one another to prevent overlapping. After the motion phase, all disks halted, and one disk turned red for 3s. Participants indicated via keyboard whether this probe was a target or a distractor. The probe could appear in either hemifield with equal probability, in the control bilateral condition. Feedback was provided at fixation, which turned green for correct and red for incorrect responses. Gaze was continuously monitored via eye tracking (see *"Eye-tracking Monitoring" section*), and any trial in which fixation was broken was immediately aborted and repeated. The stimuli were presented using the psychophysical toolbox PsychoPy 2022.2.0. The experimental setup utilized a 24-inch display (Vpixx EEG) with a resolution of 1920×1080 pixels, 8-bit RGB color depth, and a 120 Hz refresh rate.

4.3.3. Study Design

Participants were randomly assigned to one of two groups in a between-subjects design. After completing the speed thresholding procedure (see *Speed Thresholding for MOT*), all participants performed a 10-minute baseline bilateral MOT task at their individual speed threshold, which remained constant throughout the experiment.

Next, participants completed a 30-minute manipulation phase that differed by group. The *experimental group* performed a unilateral right-field MOT task, while the *control group* performed a bilateral MOT task. In the unilateral condition, participants tracked two target dots among distractors presented only in the right visual hemifield, while ignoring stimuli in the left hemifield. In contrast, in the bilateral condition, participants tracked two target dots in each hemifield simultaneously. The two conditions for the experimental and control groups were equated for difficulty because subjects were tested at their individual speed thresholds, which were measured at baseline. The task was gaze-contingent; any deviation from central fixation resulted in trial abortion and restart. Following the manipulation phase, all participants completed a 10-minute post-manipulation bilateral MOT test to assess changes in attentional performance.

4.3.4. EEG acquisition

EEG data were continuously acquired at a sampling rate of 1000 Hz using active electrodes from the Brain Products actiCAP system, and BrainVision software was used for EEG recording. A total of 64 scalp electrodes were positioned according to the extended 10–20 system (Fp1, AF3, AF7, F1, F3, F7, FC1, FC3, FC5, FT7, C1, C3, C5, T7, CP1, CP3, CP5, TP7, P1, P3, P5, P7, PO3, PO7, O1, Fp2, AF4, AF8, F2, F4, F8, FC2, FC4, FC6, FT8, C2, C4, C6, T8, CP2, CP4, CP6, TP8, P2, P4, P6, P8, PO4, PO8, O2, FPz, AFz, Fz, FCz, Cz, CPz, Pz, POz, Oz). The system employed two sets of actiCAP snap electrodes connected to two pairs of BrainAmp DC amplifiers. Two EEG caps, measuring 56 cm and 58 cm, were used for data collection, tailored to the participant's head measures. Electrode impedances were maintained below 20kΩ. Cz served as the ground, while Fz was used as the reference electrode. EEG was collected before (pre), during, and after the attentional isolation procedure.

4.3.5. Speed Thresholding for MOT

At the beginning of each session, participants’ speed thresholds for the MOT task were determined using a psychophysical staircase procedure. A 2AFC paradigm with fixed step sizes was employed to identify the motion speed corresponding to ~70% accuracy. The staircase increased stimulus speed by 0.5 cm/s following two consecutive correct responses and decreased it after a single incorrect response. This adaptive procedure continued until 15 reversals were reached. To ensure a stable estimate of tracking performance, only the final six reversals were used to compute the individual threshold. Before threshold estimation, participants completed a 120-second bilateral MOT practice block at a constant speed of 3.5 cm/s.

4.3.6. Eye-Tracking Monitoring

The EyeLink 1000 Plus system (SR Research) continuously tracked gaze position. Calibration and validation were conducted at the beginning of each run. A 3° × 3° boundary box was displayed around the central fixation point. Trials were automatically restarted if the gaze deviated outside this area to ensure compliance with central fixation throughout the task.

4.3.7. EEG data analysis

EEG data preprocessing was performed using Python (3.9.21) and the MNE-Python library (1.8.0) - (Gramfort et al., 2013). Recordings were imported from raw files in BrainVision, and all signals were re-referenced offline to the common average. A standard 10-20 electrode layout was applied to ensure consistent channel localization across datasets. Data were then downsampled to 250 Hz to reduce computational load while preserving the spectral resolution needed for subsequent analyses. Channels exhibiting artifacts or signal loss during data acquisition were identified and removed prior to re-referencing and independent component analysis (ICA) and were subsequently interpolated to preserve spatial information. On average, 2.8 channels per subject were removed and subsequently interpolated.

Continuous EEG signals were filtered using a band-pass filter from 1 to 100 Hz to remove low-frequency drifts and high-frequency noise, and a notch filter was applied at 50 Hz to suppress line noise. Following filtering, ICA was performed using the *Picard* algorithm with a number of independent components extracted equal to the number of channels retained. The decomposition was computed on continuous data. Each independent component was classified using the ICLabel algorithm (Pion-Tonachini et al., 2019), which assigned probabilistic labels corresponding to typical artifact sources such as *ocular, cardiac, muscular,* or *channel noise*. The assigned labels and their associated probabilities were retained to guide subsequent artifact rejection based on the algorithm's probabilistic classification. Specifically, artifact components with assigned probability > 95% were rejected. ICA topographies were exported for manual inspection, and ICA solutions were saved. On average, 3.72 components per subject were removed (SD = 2.96). To guarantee accurate temporal correspondence across modalities, trials lacking a valid EEG event marker were removed. The final dataset included only trials showing a one-to-one match between behavioral responses and EEG triggers. Two subjects were discharged from the analysis due to errors in trigger recording.

Continuous EEG data were segmented into epochs time-locked to the stimulus onset, spanning from −200 ms to 500 ms. The pre-stimulus interval (−200 to 0 ms) was used for baseline correction, and a linear detrend was applied to reduce slow drifts. Target identity and behavioral outcome were determined from events occurring after stimulus onset and were used to classify each target appearing-locked epoch into behavioral conditions. Specifically, for each epoch, the subsequent sequence of triggers was inspected: a left-target event followed by a correct response defined a *left-correct* trial, whereas a left-target event followed by an incorrect response defined a *left-wrong* trial. An analogous procedure was applied to right-target trials, yielding *right-correct* and *right-wrong* conditions. This classification was based on the temporal ordering of the digital trigger stream, ensuring that only epochs in which a target event and its immediate behavioral outcome followed the initial balls appearing marker were retained. All condition-specific epochs were stored separately for subsequent ERP and statistical analyses.

No a priori amplitude rejection was applied up to this point in the preprocessing pipeline. To identify and remove noisy epochs, a global rejection threshold was estimated for each participant using the *autoreject* package. Autoreject is an automated algorithm for detecting and repairing contaminated single-trial MEG and EEG data, replacing manual inspection with a reproducible, data-driven approach. It automatically determines optimal peak-to-peak thresholds—globally—using cross-validation and Bayesian optimization to identify extreme fluctuations without manual tuning (Jas et al., 2017). The computed threshold was then used to exclude epochs with signal amplitudes exceeding the estimated cutoffs. The proportion of rejected epochs was calculated and stored for each participant to assess signal quality. Specifically, we rejected on average 4.61% of epochs across subjects (SD = 9.68). This approach ensures consistency and objectivity in artifact removal across subjects, while accounting for inter-individual variability in EEG noise levels. On average, 85.20 trials per subject per session were extracted: 31.29 *left-correct*, 11.84 *left-wrong*, 27.00 *right-correct*, and 15.29 *right-wrong* trials. ERP amplitudes for all components (P1, N1, P2, N2, N2pc) were extracted using predefined temporal windows and ERP components were quantified over predefined regions of interest, with the P1 extracted from occipital–parieto-occipital electrodes (O1, O2, Oz, PO7, PO8), the N1 from a broader parieto-occipital cluster (P1–P8, Pz, PO3, PO4, POz, PO7, PO8, O1, Oz, O2), the P2 from fronto-central sites (FC1, FC2, Fz), the N2 from fronto-central–central electrodes (FC1, FC2, Fz, Cz) and the N2pc from posterior lateral electrodes (P7, P8, PO7, PO8). For each subject, session, and condition, the preprocessed epochs were cropped to the time window of interest, limited to the selected electrodes, and averaged time points to obtain a mean amplitude per electrode. The time windows for ERP components were defined as follows: P1 (80–130 ms; Hillyard & Anllo-Vento, 1998), N1 (140–200 ms; Hillyard & Anllo-Vento, 1998), P2 (170–250 ms; Cohen et al., 2024), N2 (200–300 ms; Lawson et al., 2012), N2pc (180-300ms; Mazza et al., 2009).

A linear mixed-effects model was fitted to ERP amplitude data using the lme4 and lmerTest packages. (Bates et al., 2014; Wickham et al., 2019) in R. The dependent variable was ERP amplitude (in µV). A *lmer* predicting ERP amplitude from the full factorial interaction of Session, Manipulation, and Visual Field, with Hemisphere as a fixed effect, and subject-level random intercepts and random slopes for Visual Field, fitted using maximum likelihood. Type-III ANOVA was applied to assess main effects and interactions. EMMs were computed for all interactions of interest, and pairwise contrasts were adjusted using the Holm correction for multiple comparisons. In addition, an exploratory brain/behavior analysis was performed to examine the relationship between electrophysiological responses and task performance. Specifically, mean ERP amplitudes were correlated with mean behavioral accuracy at the participant level using Pearson's correlation coefficient, averaged for condition and session.

4.3.8. Behavioral Data Analysis

Statistical analyses were performed in RStudio using the *tidyverse* and *lme4* packages (Bates et al., 2014; Wickham et al., 2019). Visualizations were generated with *ggplot2* (Wickham, 2016) while task accuracy was modeled using *glmer* with a binomial link function. Outliers in baseline performance within each Manipulation condition were identified and excluded using the 1.5×IQR method.

The fixed effects included Manipulation (*attended, ignored, contro*l), Session (*Pre, Post*), and their interaction. The random effect's structure was selected by comparing models with different random slopes. Fixed effects were evaluated via Type III Wald chi-square tests. Estimated marginal means (EMMs) were computed for each Session × Manipulation combination using the *emmeans* package. Within-condition changes across sessions (Post − Pre) were quantified as *delta scores*. Pairwise contrasts between *delta scores* were used to assess differential effects of Manipulation. *Holm* correction was applied to adjust for multiple comparisons.

To track post-manipulation changes while accounting for baseline differences, baseline accuracy (*PreScore*) was computed for each participant and manipulation condition as the mean accuracy in the *pre-session*. A binomial GLMM was fitted with *Manipulation* as a fixed effect, *PreScore* as a covariate, and a random intercept for *Subject*. Baseline-adjusted marginal means were derived from the model, and pairwise contrasts were performed with *Holm* correction. While delta scores (Post - Pre) were initially used to provide a preliminary overview of raw performance changes, this approach is often limited by regression toward the mean and potential ceiling effects. To account for heterogeneous baseline levels, we implemented a GLMM including *PreScore* as a fixed effect. This allowed us to statistically equate participants at the starting point and partition out initial variance, providing a more robust and sensitive measure of the manipulation's true effect on the performance trajectory (Lord, 1967; Vickers & Altman, 2001).

4.4. Results

4.4.1. Preliminary behavioral results

We first checked for outliers in the pre-test conditions for all subjects. No outliers were detected, leaving 37 subjects for statistical analysis (19 in the Control group and 18 in the Ignored group).

Subsequently, we computed delta changes (Post – Pre) for each condition. The g*lmer* model revealed a two-way interaction between session and manipulation ($\chi^2(1) = 7.43$, $p < .01$, $n = 37$, *glmer*). EMMs were then computed for all session × manipulation combinations, and planned comparisons were performed using pairwise contrasts. Finally, pairwise deltas were adjusted for multiple comparisons using the Holm correction. Results show a significant difference between the delta change in the ignored condition and the control condition (estimate= -0.36, se=0.13, z=-2.68, p <. 05, OR = 0.70, 95 % CI [0.51, 0.96]), indicating a change of the tracking performance in the control condition compared to the ignored condition, while there was no significant change between the delta changes in the attended vs ignored (estimate= -0.30, se=0.15, z=-2.05, p>.05, OR = 0.73, 95 % CI [0.51, 1.06]) and between the delta changes in the attended visual field and control (estimate= 0.05, se=0.12, z=0.43, p>.05, OR = 1.05, 95 % CI [0.77, 1.43]) – (Figure 16). Specifically, the delta in the Ignored condition was higher than in the Control condition, indicating a significant difference in tracking accuracy following the manipulation.

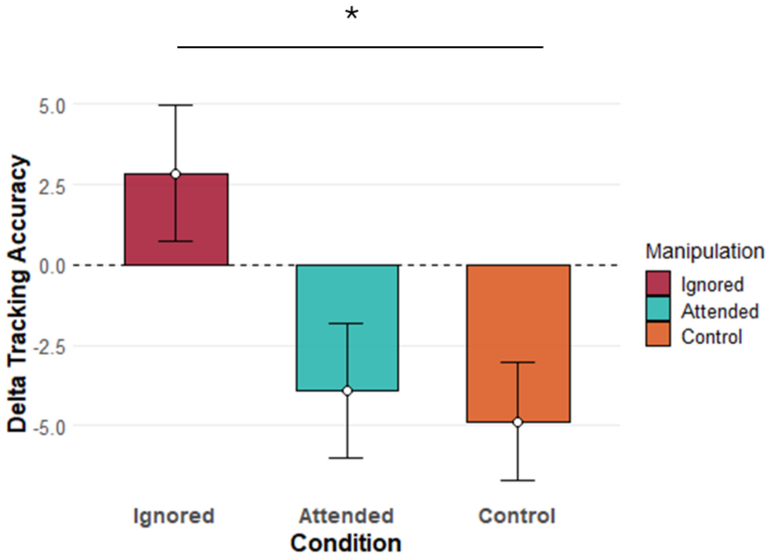


Figure 16 - *Delta changes in performance (Post–Pre) across the three manipulation conditions (Ignored, Attended, Control). Performance in the Ignored visual field was significantly higher than in the Control condition (p < .05). No significant differences were observed for the Attended visual field (p>.05). Standard error is reported.*

Building upon this, to account for potential baseline differences among participants, we fitted a generalized linear mixed-effects model (GLMM) including *PreScore* as a fixed effect. The model revealed significant main effects of manipulation ($\chi^2(2) = 16.36$, $p <$ .001, n = 37, *glmer*) and PreScore ($\chi^2(1) = 40.64$, $p < .001$, n = 37). Holm-corrected post hoc comparisons showed that, post manipulation, the accuracy in the ignored visual field was significantly higher than in the attended visual field (estimate = –0.43 ± 0.11, $z = –3.92$, $p = < .01$, OR = 0.64, 95 % CI [0.50, 0.84]). These results point toward higher performance following the isolation period in the ignored visual field compared with the attended visual field. Furthermore, a significant difference between the control and the ignored visual field was reported, pointing towards a higher performance in the ignored visual field (estimate = –0.34 ± 0.13, z = –2.58, p < .05, OR = 0.71, 95 % CI [0.52, 0.98]). Importantly, there was no significant difference in performance between the control and the attended visual field (estimate = -0.09 ± 0.13, z = –0.71, p >.05, OR = 0.91, 95 % CI [0.66, 1.24]) In other words, the effect of the isolation was specific to the ignored visual field, with no effect on either the attended visual field or the control condition.

4.4.2. Preliminary EEG results

Before conducting the EEG analysis, two participants were excluded from the initial sample of 37 due to technical issues during data acquisition, resulting in a final sample of 35 subjects (Control = 17, Ignored = 18). Subsequently, an lmer was used to estimate ERP amplitudes as a function of the full session × group × manipulation interaction.

Components	**Group**	**Visual Field**	**Pre Mean ± SD (µV)**	**Post Mean ± SD (µV)**
N1	BI	Left	-0.96 ± 4.28	-0.75 ± 4.56
N1	BI	Right	-0.93 ± 4.40	-1.10 ± 4.48
N1	UR	Left	-1.40 ± 4.12	-0.97 ± 3.94
N1	UR	Right	-1.10 ± 4.01	-0.64 ± 3.83
N2	BI	Left	0.01 ± 3.23	0.45 ± 3.27
N2	BI	Right	0.20 ± 3.24	0.40 ± 3.26
N2	UR	Left	0.01 ± 3.09	0.26 ± 3.09
N2	UR	Right	0.07 ± 3.09	0.24 ± 2.93
P2	BI	Left	-0.01 ± 4.01	0.29 ± 4.12
P2	BI	Right	0.25 ± 3.80	0.26 ± 3.95
P2	UR	Left	0.38 ± 3.44	0.49 ± 3.55
P2	UR	Right	0.38 ± 3.42	0.30 ± 3.39
P1	BI	Left	-0.75 ± 5.04	-0.81 ± 4.83
P1	BI	Right	-0.99 ± 4.85	0.56 ± 5.10
P1	UR	Left	-1.13 ± 4.31	-1.09 ± 4.10
P1	UR	Right	-0.68 ± 4.20	-0.41 ± 4.22
N2pc	BI	Left	-1.03 ± 2.79	-1.19 ± 2.86
N2pc	BI	Right	-0.58 ± 2.94	-0.71 ± 3.30
N2pc	UR	Left	-0.70 ± 3.08	-0.75 ± 2.77
N2pc	UR	Right	-1.06 ± 2.90	-1.01 ± 2.77

***Table 2** – Descriptive table reporting, for each ERP component, the mean amplitude (expressed in uV) and standard deviation, stratified by group, visual field, and session (Pre and Post).*

Hemisphere was included as a fixed effect, and subject-specific random intercepts and random slopes for visual field were allowed. The model was fitted using maximum likelihood. A significant session × manipulation interaction was found for the N1 component ($\chi^2(1) = 7.36$, $p <.05$, $n = 35$, glmer), indicating that changes in N1 amplitude across sessions depended on the specific manipulation condition.

Follow-up analyses using estimated marginal means with Holm-corrected post hoc contrasts revealed that N1 amplitudes became significantly less negative from pre- to post-session in both the ignored visual field (estimate = 0.33 µV, se = 0.10, t(29,787) = 3.45, $p < .05$) and the attended visual field (estimate = 0.41 µV, se = 0.09, t(29,855) = 4.30, $p < .05$) in the UR group. No significant interactions were observed for the P1, P2, N2 or N2pc components (all $p > .05$) - (Figure 17A-B). Furthermore, a significant positive correlation was observed between mean N1 amplitude and behavioral accuracy ($r = 0.41$, $p < .05$), indicating that reduced N1 amplitudes were associated with higher task performance (Figure 17C).

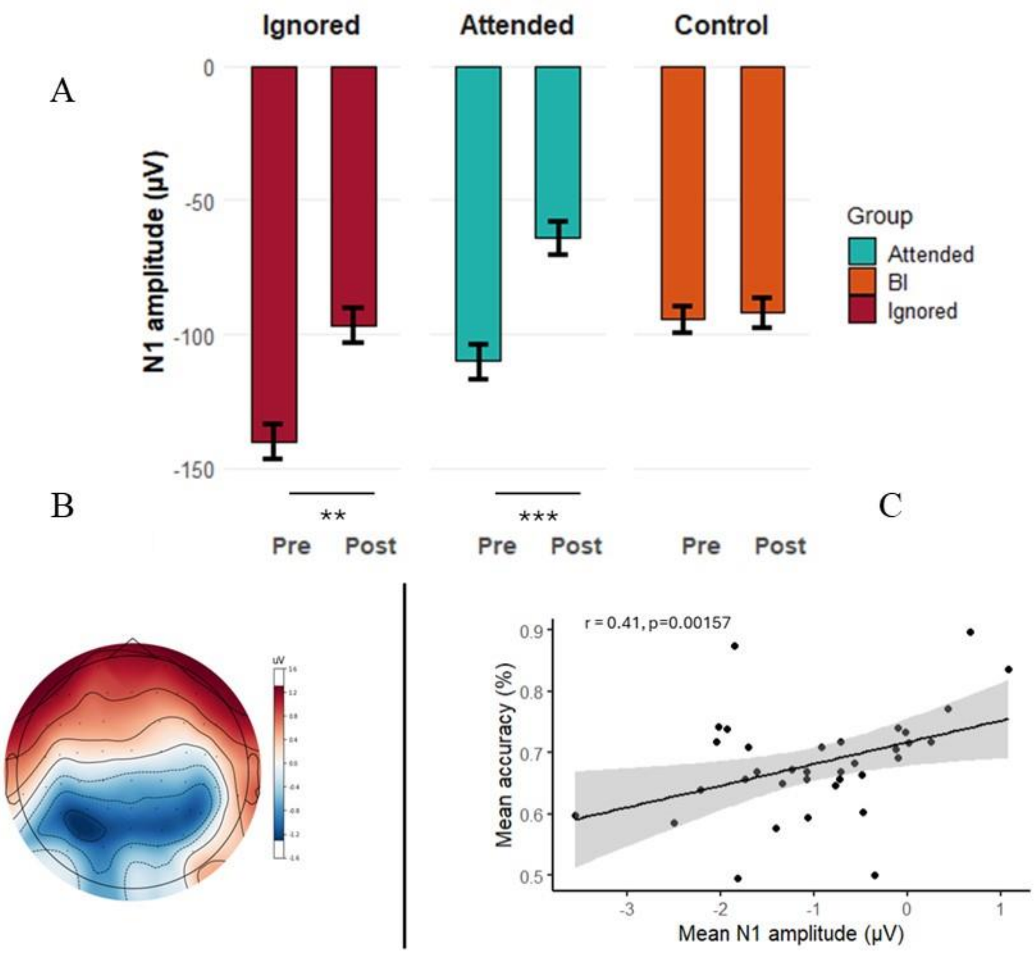


Figure 17 - (A) *N1 amplitude changes are shown across Manipulation conditions (attended, control, ignored) and Sessions (Pre, Post). A reduction in N1 negativity from pre to post is observed in the ignored and attended visual fields, whereas no significant changes are detected in the control condition. Averaged tracking accuracy performance is reported as a function of the manipulation condition and the session.* ***(B)*** *Grand-average N1 scalp topography, averaged across subjects and experimental conditions, is displayed in the 180–300 ms time window.* ***(C)*** *Pearson correlation between N1 amplitude and behavioral performance in the MOT task is shown, with both measures averaged across subjects and experimental conditions.*

4.4.3. Preliminary conclusions

Our experimental data are consistent with previous studies showing that a period of attentional isolation applied to one hemifield (attended) leads to a paradoxical improvement in attentional performance in the contralateral hemifield (ignored) - (Edwards et al., 2021, and Chapter 3). We observed that the benefit in the MOT task was only present in the attentional isolation experimental condition and absent in the control group. This study is the first to investigate the neural basis underlying the attentional isolation procedure. Previous accounts of this phenomenon have relied on speculative explanations, such as changes in cortical excitability or homeostatic control mechanisms (Edwards et al., 2021). Using EEG recordings, we provide the first experimental evidence that supports these hypotheses. Following attentional isolation, for example, trials presented in the ignored visual field exhibited a significant reduction in N1 ERP amplitude compared to the pre-manipulation period. This effect was strictly identified by the N1 wave; no significant modulations were observed in the P1, P2, or N2 components. Interestingly, we also observed a decrease in N1 amplitude for trials shown in the attended visual field. However, this neural change did not translate into a clear behavioral correlation; in fact, accuracy in the attended field remained lower compared to the ignored visual field following the attentional procedure (after controlling for the baseline, *PreScore analysis*). These findings present a nuanced electrophysiological landscape. The reduction in N1 amplitude following attentional isolation, specifically for trials in the ignored visual field after controlling for hemispheric fixed effects, suggests a mechanism of neural optimization (Budd et al., 1998; Davies et al., 2010; Roussel et al., 2014; J. N. Vickers, 1996; D. L. Woods & Elmasian, 1986). This likely reflects the "attentional rebound" effect, where the brain reorganizes perceptual resources to process previously suppressed information more efficiently. Our preliminary correlation analyses support this interpretation, revealing a significant positive association between N1 amplitude and tracking accuracy: less negative amplitudes were associated with superior performance. This aligns with the hypothesis that behavioral gains in tracking are driven by an early attentional optimization rather than a simple increase in sensory gain.

The observed N1 reduction in the attended visual field, however, likely stems from a divergent parallel process. While the ignored field benefits from enhanced cognitive efficiency and plastic reorganization, the attended field may be undergoing sensory adaptation or habituation due to the 30-minute task practice. This mirrors a critical distinction found in the literature, where N1 modulations can represent either a functional suppression of unattended inputs or a signature of high-level learning transfer (G. L. Zhang et al., 2013). In our case, the electrophysiological reduction appears to generalize across both fields, yet the behavioral manifestation of this efficiency is only detectable in the "rebound" of the ignored field.

Given the preliminary nature of these data, the N1 amplitude in the attended field and its lower behavioral performance compared to the ignored might reflect either a "ceiling effect" in practice or inherent noise obscuring the brain-behavior relationship. To further parse these effects, future analyses should employ empirical cut-offs or cluster analysis to categorize subjects who exhibited a robust rebound effect (e.g., Zhang et al., 2013, who used a similar approach). By isolating these "high-responders," we could potentially determine whether the neural efficiency generalizes or if a clear performance decrement exists in the attended field. Further investigations into time-frequency and connectivity patterns are essential to move beyond surface-level observations. Such analyses would help us identify the underlying homeostatic mechanisms and the general network reorganization triggered by attentional isolation.

To conclude, this pattern aligns with prior ERP and neuroimaging studies indicating that training-related performance gains frequently coincide with diminished neural responses, suggesting enhanced processing efficiency rather than reduced engagement (Budd et al., 1998; Grill-Spector et al., 2006; A. M. C. Kelly & Garavan, 2005; D. L. Woods & Elmasian, 1986) . Importantly, the N1 component has been widely associated with perceptual selection mechanisms and the resolution of sensory competition (Vogel & Luck, 2000). In this framework, the observed N1 reduction in the presence of improved behavioral performance is compatible with a facilitatory reorganization of perceptual-attentional processing.

5. CHAPTER 5: Final remarks

5.1. Overview of the thesis

5.1.1. General discussion

In this final chapter, we offer a brief, critical overview of the findings presented in this thesis, emphasizing the theoretical and practical implications and possible limitations. Specifically, we clarified the role of a behavioral procedure, called attentional isolation, in modulating visuospatial performance on the MOT task, and how NIBS can affect this procedure, revealing the dynamics of interhemispheric competition. To provide an initial overview of the topic, Chapter 2 presents a comprehensive systematic review of how NIBS and neuroimaging can be combined to study visuospatial attention. This study shows that combining these methodologies has shifted experimental paradigms from correlational approaches to paradigms capable of investigating network-level dynamics and related behavioral outcomes. The literature commonly shows that behavioral investigations are widely supported by changes in functional connectivity and network oscillations, demonstrating the growth of these methodologies over the years. However, a heterogeneous landscape also emerged, with inconsistencies between methodologies and studies showing a potential gap in the field. In Chapter 3, we studied how NIBS, specifically tRNS, can modulate interhemispheric competition. This allows us to clarify the role of the right and left hemispheres in the attentional isolation paradigm, also observed in previous work (Edwards et al., 2021). Our results showed a clear hemispheric asymmetry resulting from tRNS modulation of attentional reallocation. Briefly, we found a dissociation between right and left hemisphere stimulation, with an improvement in the ignored visual field persisting only after left frontoparietal stimulation. Conversely, right stimulation abolished the attentional isolation effect, disrupting the rebound effect. These results align with the current literature emphasizing asymmetry in attention allocation, which is more pronounced in the right hemisphere than the left. This explains why right hemisphere stimulation generally suppresses the effect, while left stimulation produces a more localized, contralateral effect (Corbetta & Shulman, 2002; Heilman & Valenstein, 1979; Heilman & Van Den Abell, 1980).

Finally, Chapter 4 presents preliminary results from neurotypical participants. It investigates the neural basis of the attentional isolation procedure and highlights a significant reduction in N1 ERP amplitude compared to the period prior to manipulation, particularly in the ignored visual field. Interestingly, the reduction in N1 amplitude predicted improved MOT tracking performance. These preliminary results seem to indicate a facilitating effect and increased system efficiency following the isolation procedure. This suggests the existence of possible homeostatic and regulatory mechanisms in the context of interhemispheric competition (Vogel & Luck, 2000).

Overall, our experimental findings indicate that the two hemispheres play distinct roles in modulating visuospatial attentional performance, particularly within the attentional isolation paradigm. Specifically, we observed a clear hemispheric dissociation following unilateral frontoparietal stimulation, suggesting that the effects of tRNS critically depend on the functional and anatomical substrates being modulated. Unilateral stimulation of the frontoparietal network may have altered the physiological asymmetry typically observed in neurotypical individuals in the visuospatial domain, which is often characterized by right-hemisphere dominance (Ten Brink et al., 2017). The right hemisphere has been consistently associated with integrative processing across the visual field; accordingly, right-lateralized stimulation may have promoted a more unified allocation of attention across hemifields, thereby reducing the magnitude of the attentional rebound effect (Kleinman et al., 2006). In contrast, left frontoparietal stimulation may have favored more segregated processing, preserving hemispheric asymmetries in attentional allocation and maintaining the rebound effect across hemifields (Fiebelkorn & Kastner, 2020; Sheremata & Silver, 2015). These results highlight the importance of lateralized stimulation, as most previous studies have relied on bilateral stimulation protocols (Contò et al., 2021, 2023; Giglia et al., 2011; Tsujimoto et al., 2022).

Over time, tRNS has emerged as a valuable tool for probing visuospatial attentional dynamics and their underlying neural contributions (Bertoni et al., 2023; Contò et al., 2021; van der Groen et al., 2022). In our study, frontoparietal tRNS allowed us to disentangle the specific contributions of the right versus left hemispheres in attentional isolation. While other tES protocols, such as tACS, often use bilateral montages to shift attentional allocation through controlled excitation and inhibition, tRNS is polarity-independent and operates via different mechanisms, such as stochastic resonance (O'Hare et al., 2021; Paulus et al., 2016; Pavan et al., 2019). Following this framework, we hypothesize that "injecting" an optimal amount of noise can enhance the neural signal clarity, whereas excessive or insufficient noise acts as a nuisance (Battaglini et al., 2023; Campana et al., 2016). Although tRNS is often categorized as inhibitory (1–100 Hz) or excitatory (101–640 Hz) based on motor cortex studies, we must acknowledge that without electrophysiological measures, we cannot definitively assert changes in cortical excitability within the IPS or FEF (Ghin et al., 2021; Moret et al., 2019). Nevertheless, we can speculate that frontoparietal tRNS suppresses attentional deployment during isolation in the right hemisphere, while potentially facilitating it in the left. This could suggest a reassessment of the DVAN, as proposed by Contò et al. (2021), and highlights the need for future studies to account for individual differences and optimal parameter settings when assessing tRNS effects on MOT performance. Importantly, we also provide initial, preliminary evidence of neural correlates underlying the attentional rebound effect. Modulations in N1 amplitude suggest a reorganization of perceptual–attentional processing, potentially reflecting facilitatory mechanisms (Vogel & Luck, 2000). This pattern is consistent with accounts of homeostatic plasticity, whereby the brain actively rebalances neural activity following prolonged periods of sensory or attentional imbalance. (Bliem et al., 2008; Federici et al., 2023; Hendy & Lamon, 2017; Mrsic-Flogel et al., 2007; Y. K. Wu et al., 2020). More broadly, this thesis underscores the importance of combining NIBS with precise behavioral measures to investigate causal relationships between neural activity and behavior. Such an approach not only allows for the identification of functional dissociations but may also have translational relevance, offering potential avenues for the development of targeted interventions in clinical populations characterized by attentional imbalances.

5.1.2. Limitations, future directions, and conclusion

Some general limitations must be examined and considered when critically analyzing the data and results reported in this thesis. Specifically, tRNS shares common limitations with other electrical stimulation techniques, as discussed in Chapter 3. As discussed in Chapter 2, there is a general trend of inconsistencies between stimulation protocols and paradigms due to individual differences, experimental settings, and the tools used by researchers. Furthermore, tRNS is not considered focal when current is delivered to the skull through large electrodes. However, when active control conditions are carefully chosen, the effects can be very selective. This indicates that while a network effect cannot be ruled out, it can still be behavioral- and network-specific (Contò et al., 2021). We acknowledge the possibility that in Chapter 3, we did not directly investigate neural mechanisms, but we have an indirect assessment of them through the use of NIBS. Directly probing neural mechanisms using tES alone remains limited due to its low spatial focality and restricted ability to target deep or specific neural structures (Huang & Parra, 2019; Karabanov et al., 2019; Saturnino et al., 2019; Seo & Jun, 2019). For this reason, multimodal approaches combining brain stimulation with neuroimaging techniques (e.g., EEG or fMRI) are increasingly employed to infer underlying neural mechanisms and network-level effects (Ramírez-Guerrero et al., 2025). Within this framework, targeting frontoparietal nodes, key components of the visuospatial attention network, has been shown to modulate hemispheric dynamics and reveal asymmetries in attentional processing, indirectly pointing to distinct underlying neural mechanisms. A further discussion of this topic is broadly provided in Chapter 2 of the manuscript, within the systematic review section. Additionally, even if the sample size is adequate, it may be useful to increase the number of participants to account for heterogeneity in responses to stimulation and manipulation. Future studies may benefit from reducing participant heterogeneity and using a more in-depth neuropsychological assessment with multiple test batteries to better understand each participant's individual functioning.

The EEG study presented in Chapter 4 contains mostly preliminary and partial data, including ERPs and brain/behavior correlations. For this reason, the results must be contextualized within the theoretical framework of attentional isolation and considered preliminary, with possible subsequent modifications or further investigation.

Current evidence suggests that the effects of tRNS are highly dependent on stimulation parameters. Future studies should therefore aim to disentangle the specific contribution of these parameters in modulating the attentional rebound effect described in this manuscript. Notably, in the present study, we did not observe a clear improvement in tracking performance following tRNS. Instead, we found a mixed, hemisphere-dependent effect, whereby tRNS appeared to either maintain or disrupt the behavioral consequences of the attentional isolation procedure. One possible interpretation is that the efficacy of tRNS may be enhanced when combined with other neuromodulatory techniques. In particular, previous work has shown that tRNS can be optimized when paired with transcranial magnetic stimulation (TMS) - (Edwards et al., 2020). In this context, tRNS may act as a priming mechanism, modulating baseline neural excitability and thereby facilitating the subsequent effects of TMS, ultimately leading to broader behavioral outcomes. This approach is consistent with the principle of metaplasticity, whereby the prior state of neural activity influences the response to subsequent stimulation.

The findings presented here provide a solid foundation for future research exploring such multimodal interventions. For example, combining tRNS with TMS may represent a promising strategy to enhance attentional performance. Specifically, high-frequency tRNS may stabilize neural activity and serve as a primer, enhancing the subsequent effects of low-frequency TMS over regions such as the IPS. As demonstrated by Edwards et al. (2020), such combined protocols can induce cortical changes associated with improved sustained attentional tracking in neurotypical individuals. Therefore, the effects of attentional isolation could be extended beyond the immediate post-manipulation effect to longer periods, to observe potential long-term changes indicating sustained effects in time, with clear translational implications. Furthermore, it would also be useful to characterize the networks primarily involved in attentional isolation using fMRI. For example, it is plausible to hypothesize changes in connectivity in both the DMN and the DVAN. Some studies could use magnetic resonance spectroscopy (MRS) to investigate neurochemical changes induced by attentional isolation and shed light on homeostatic mechanisms regulating interhemispheric competition. Further studies could also examine the attentional isolation procedure as a potential add-on intervention in clinical rehabilitation in neurological patients with attentional deficits. A preliminary, unpublished study from our lab examined the efficacy of a 30-minute attentional isolation manipulation to improve visual attention in right-hemisphere stroke patients (Edwards et al., 2022). The researchers found that participants with mild or no initial leftward inattention showed significantly better accuracy in MOT after the intervention compared to a control condition, indicating an enhancement of sustained attention across the entire visual array. However, this behavioral gain was not observed in patients with more pronounced leftward inattention. These findings provide a "proof of concept" for non-invasive rehabilitation strategies that leverage the unaffected visual space to modulate lateralized attention processing after a stroke.

Finally, the attentional isolation paradigm is conceptually inspired by established frameworks such as monocular deprivation and motor paradigms of cross-training or cross-education. While important distinctions must be maintained — given the differing cognitive and neural substrates involved — it is plausible that these paradigms share common underlying principles related to homeostatic plasticity. At present, however, direct empirical evidence linking attentional isolation with monocular deprivation remains absent. A logical next step would be to adopt a multimodal approach similar to that used in the monocular deprivation literature. This would include EEG investigations featuring ERP, time–frequency, and source reconstruction analyses, followed by fMRI or magnetic resonance spectroscopy (MRS) to assess changes in neurochemical markers such as GABA and Glx, which are associated with homeostatic balance and plasticity mechanisms (Binda et al., 2018; Lunghi, Emir, et al., 2015).

In conclusion, this manuscript demonstrates how attentional isolation and NIBS can modulate and dissociate the roles of the two cerebral hemispheres, thereby highlighting their differences in the context of hemispheric competition theory. These promising findings, further supported by EEG and patient studies, reveal the underlying mechanisms of homeostatic regulation and the plasticity of visuospatial attention and functioning.

Declaration of generative AI and AI-assisted technologies in the writing process

During the drafting and revision phases of this thesis, writing assistance tools (Grammarly, Claude, and DeepL) were used to improve the readability and grammatical correctness of the manuscript. The content was subsequently checked, edited, and validated by the author.

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