



## Investigating the attentional state dependency of interhemispheric interactions - a TMS-EEG study

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One of the most influential models of attentional control posits that we fully perceive our surroundings because the two cerebral hemispheres, each directing attention toward the contralateral side of space, are kept in balance through reciprocal interhemispheric inhibition [1]. Evidence for the *rivalry model* [1] comes from studies of patients with spatial neglect, in whom a lesion to the right posterior parietal cortex (PPC), a key node of the attentional network, results in a loss of awareness of the contralesional (typically left) side of space [2]. Such lesions not only reduce local activity in the damaged hemisphere but also result in hyperactivation of the left hemisphere, due to the release of right-to-left inhibition [1]. Notably, neglect symptoms are often ameliorated by inhibition of the left, hyperactive, PPC and are accompanied by a rebalancing of the interhemispheric equilibrium [3,4]. Neglect behavior has been successfully modeled in healthy individuals using both so-called inhibitory repetitive transcranial magnetic stimulation (rTMS) over the right PPC [5] and leftward prism adaptation [6], a visuomotor training, that depending on the direction of the visual displacement, either alleviates neglect symptoms or induces neglect-like biases in healthy individuals. However, when neural changes were assessed using resting-state fMRI the expected push-pull pattern between the PPCs did not emerge [5,6]. In contrast, when those were quantified while participants were engaged in a visual attention task a differential effect was found - receptive field size increased in the left but not right PPC [7].

Based on this evidence, we investigated whether the interhemispheric rivalry is a default feature of the attentional system or whether it depends on the state of the attentional network. We hypothesized that interhemispheric dynamics underlying attentional processing depend on the level of attentional engagement (i.e., state) and expected the push-pull pattern to emerge in healthy brains when the attentional system is actively recruited.

Twenty-two righthanded, healthy young adults participated in the within-subjects experiment consisting of a single TMS-EEG co-registration session, preceded by the Landmark task to quantify visuospatial bias and interhemispheric dominance (Fig. 1A). During the session, single TMS pulses were delivered over the right and left PPC (Fig. 1B) while

participants were engaged in a visual task designed to elicit two different level of attentional engagement - attention vs. detection condition (Fig. 1C) [7]. See Supplementary Materials for details.

Concerning the visuospatial bias, the group showed the leftward bias indicating a right hemisphere dominance typical of young individual (Supp. Fig. 1A) that however did not differ from zero ( $p > 0.05$ ,  $d = -0.234$ ), since 1/3 of the participants exhibited a rightward spatial bias (Supp. Fig. 1B).

To assess hemispheric differences, we investigated TMS-evoked potentials (TEPs) modulations under the two attentional states. We compared TEPs elicited by left vs. right PPC stimulation separately for the attention and detection conditions using cluster-based permutation testing. As expected, a significant cluster indicating a difference in TEPs amplitude between stimulation sides was found in the attention ( $p < 0.048$ ) but not detection condition (Fig. 1D). This effect emerged 43–86ms post-stimulation over frontal electrodes contralateral to stimulation and was characterized by higher TEPs amplitudes following left as compared to right PPC stimulation. No differences in interhemispheric signal propagation (ISP) values emerged between conditions, regardless of stimulation side regional comparison (parietal and frontal;  $P_s > 0.05$ ), as well as no correlation with the visuospatial bias for either stimulation side or condition ( $P_s > 0.05$ ). This null result may reflect ISP metric greater sensitivity to strongly bilateral circuits than to more asymmetric higher-order network.

The presence of a difference between left and right hemisphere TEPs exclusively in the attention condition, supports the hypothesis of an interhemispheric dynamic within the visuospatial attentional network that is modulated by the level of attentional engagement. This effect is unlikely to be driven by task performance since participants achieved high and consistent accuracy across all conditions [7] ( $P_s > 0.05$ ; Supp. Fig. 2).

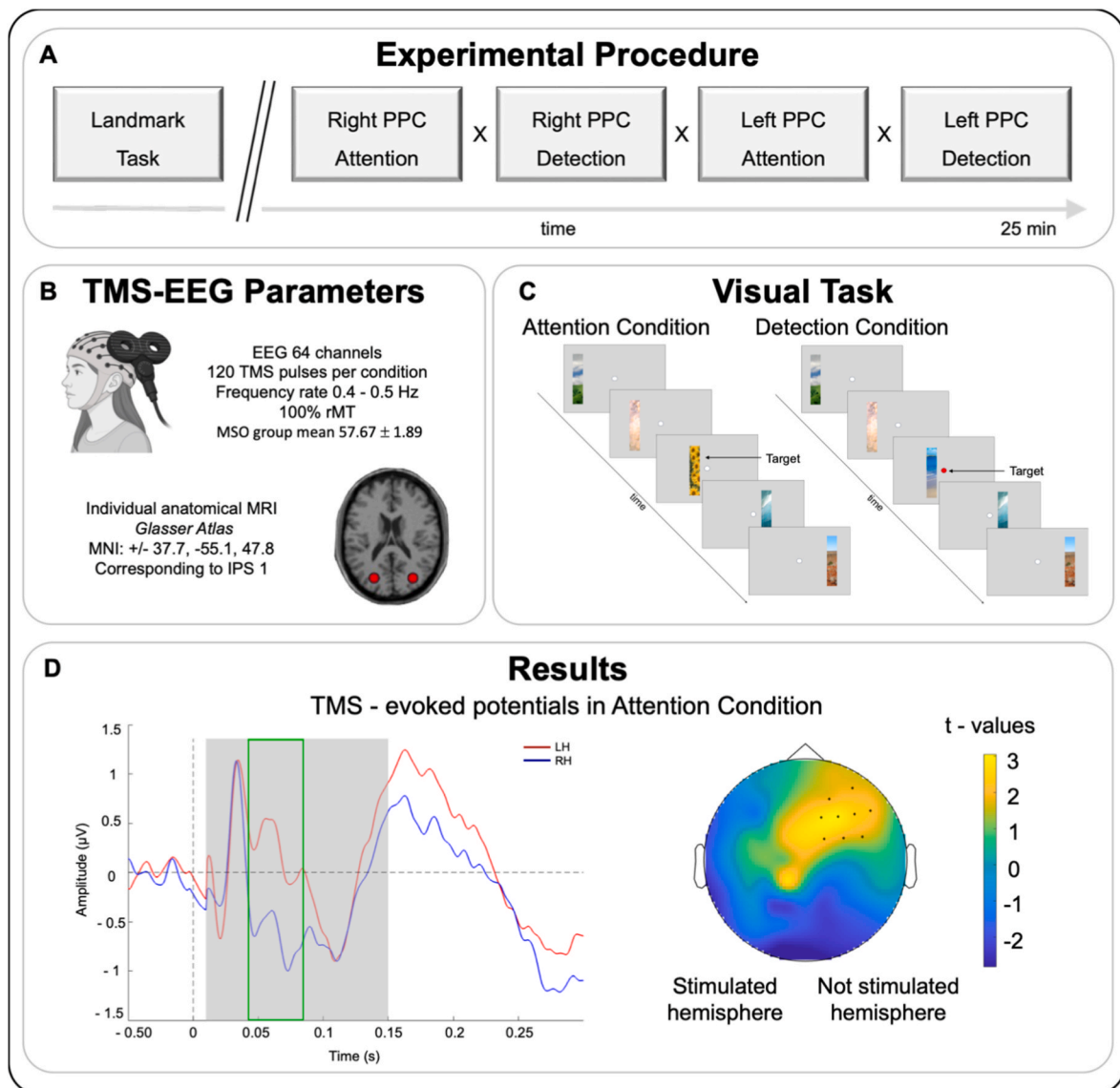
Surprisingly, the TEPs analysis did not reveal interhemispheric interaction between homologous areas (i.e., parieto-parietal). Instead, the finding pointed to an interhemispheric dynamic between parietal cortices and their contralateral frontal regions, both of which are however key nodes of the dorsal attentional network. This pattern could be explained by findings of a previous study from our group [5], which

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**Fig. 1. A. Experimental procedure.** Landmark task was administered prior any TMS-EEG co-registration to quantify the visuospatial bias and infer hemispheric dominance. During the TMS-EEG co-registration, consisting of four consecutive blocks, single-pulse TMS was delivered over the right and left PPC while participants were engaged in a visual task demanding two different levels of attentional deployment. Stimulation sites and visual task conditions were counterbalanced across participants. **B. TMS-EEG Parameters.** TMS and EEG parameters used in the study. Mean and standard error of the mean of the MSO (maximum stimulator output) used. **C. Visual Task.** It was administered during the TMS-EEG co-registration to induce two different attentional states (attention vs. detection condition). Stimuli were displayed through a bar aperture that gradually moved across the visual field, revealing segments of scenes. In the attention condition, participants searched for a specific target scene fragment (e.g., yellow sunflowers) and pressed the spacebar when they saw it. In the detection condition, they pressed the spacebar when the central dot turned red. **D. Results.** TEPs recorded during left and right hemisphere stimulation were compared for each attentional condition between 10 and 150ms post-pulse (grey shaded area). A significant cluster, localized over frontal electrodes contralateral to stimulation, emerged between 43 and 86ms post-stimulation and indicated higher TEPs amplitudes following left as compared to right PPC stimulation for the attention but not detection condition. Early TEP deflections ( $\sim 10$ – $20$ ms) appear different across conditions but did not yield a significant cluster, likely reflecting brief and inconsistent effects across participants.

using resting-state fMRI, showed that inhibitory rTMS over the right PPC induces neglect-like behavior in healthy brains and alters interhemispheric functional connectivity between right PPC and left superior temporal gyrus (STG). Since STG has been implicated in the pathophysiology of neglect [9] and it exerts modulatory influence on the dorsal network [8] it could be responsible for integrating the ventral and dorsal attention network through its connections with frontal regions. This proposed framework might account for the interhemispheric fronto-parietal activation observed in present study, coherently with the timing of the observed cluster (43–86ms) which may indicate the involvement of subcortical connections.

Finally, the reason why, solely in the attention condition, stimulation

of the left PPC induced larger TEPs than stimulation of the homologous could be related to the asymmetry in PPC to PPC inhibition - the right-to-left inhibition is stronger than the left-to-right one [10]. In the condition of attentional deployment, the right hemisphere is actively engaged, and as attentional demand increases, so does the inhibitory influence exerted by the right PPC onto the left. It is therefore possible that, when TMS is applied to the left PPC, it not only perturbs local processing but also transiently interrupts the inhibition exerted by the right PPC/hemisphere. By releasing this inhibitory control, right-hemisphere frontal regions activity further increases, thereby aiming to modulate the left PPC and contributing to a rebalancing of interhemispheric dynamics.

However, interpretation of the interhemispheric effect could be

hindered by variability in visuospatial bias, and thus hemispheric dominance, as well as by the limited EEG spatial resolution, which prevents assessing subcortical contributions. Moreover, single-session data collection prevented the assessment of test–retest reliability and reproducibility.

In conclusion, this study provides the first evidence of an asymmetric, state-dependent, interhemispheric dynamic in intact brains. Our finding indicates that the functional state of the attentional system modulates interhemispheric interactions, which may ultimately inform targeted rehabilitation strategies for individuals with unilateral attentional deficits.

#### CRediT authorship contribution statement

**Arianna Brancaccio:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation. **Cora M. Lanza:** Writing – review & editing, Writing – original draft, Project administration, Investigation, Data curation. **Selene Schintu:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Formal analysis, Conceptualization.

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#### Declaration of competing interest

The authors declare no conflict of interest.

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#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.brs.2025.103011>.

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