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RESEARCH ARTICLE

Hemispheric functional segregation facilitates target detection during sustained visuospatial attention

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Abstract

Visuospatial attention is strongly lateralized, with the right hemisphere commonly exhibiting stronger activation and connectivity patterns than the left hemisphere during attentive processes. However, whether such asymmetry influences inter-hemispheric information transfer and behavioral performance is not known. Here we used a region of interest (ROI) and network-based approach to determine steady-state fMRI functional connectivity (FC) in the whole cerebral cortex during a leftward/rightward covert visuospatial attention task. We found that the global FC topology between either ROIs or networks was independent on the attended side. The side of attention significantly modulated FC strength between brain networks, with leftward attention primarily involving the connections of the right visual network with dorsal and ventral attention networks in both the left and right hemisphere. High hemispheric functional segregation significantly correlated with faster target detection response times (i.e., better performance). Our findings suggest that the dominance of the right hemisphere in visuospatial attention is associated with an hemispheric functional segregation that is beneficial for behavioral performance.

KEYWORDS

covert attention, functional connectivity, hemispheric segregation, reaction times, steady-state fMRI, task performance

1 | INTRODUCTION

Human brain is organized according to stereotypical patterns of hemispheric functional segregation, that is, the reduction in the strength of inter-hemispheric functional connectivity (FC) (Ailion et al., 2022; Davis & Cabeza, 2015; Gabitov et al., 2019), whereby cognitive functions are asymmetrically distributed (Vingerhoets, 2019). The hemispheric functional segregation is thought to confer selective advantage in terms of efficiency and redundancy of brain circuits, which in turn affect behavioral performance (Levy, 1977; Vallortigara, 2006). For instance, the human brain constantly receives

more visual information than it can simultaneously process, and the selection of the most relevant stimuli is performed by visuospatial attention mechanisms that are strongly dominated by the right hemisphere (Corballis, 2003). Thus, left hemifield stimuli are known to be processed more quickly and accurately than right hemifield stimuli, a phenomenon known as pseudo-neglect (Bowers & Heilman, 1980; Jewell & McCourt, 2000).

Besides strongly affecting the processing of visual inputs (e.g., see Watanabe et al., 2011), there is evidence that visuospatial attention also affects FC of large scale networks at the whole-brain level (Spadone et al., 2015; Szczepanski et al., 2013). In particular, attention

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modulates the connectivity strength (i.e., the degree of linear correlation, or the intensity of association) between sensory (e.g., visual and/or auditory) and dorsal/ventral attention cortical networks, without substantially changing the overall topology (i.e., the actual connectivity patterns, or the structure of the network) of the functional connections (Betti et al., 2013; Favaretto et al., 2021; Spadone et al., 2015). Yet, some results suggest that the structure of the involved brain networks is also dynamically changed (Bray et al., 2015). Thus, inconsistencies in previous work make it difficult to predict how any asymmetry in FC patterns and ensuing differences in inter-hemispheric information transfer might impact behavior.

In healthy subjects, functional segregation of the ipsilateral and contralateral somatomotor cortex during motor skill acquisition has been found to be correlated with performance gains (Gabitov et al., 2019). Similarly, inter-hemispheric communication between bilateral superior temporal gyrus during verbal tasks has been associated with slow performance in children (Bitan et al., 2010). Altered inter-hemispheric connectivity has also been found to be correlated with aging and the decline in executive functions (Zhao et al., 2020). A better comprehension of the mechanisms for attention lateralization and their relation to behavioral and cognitive states might help to shed light on the pathophysiology of attention deficit disorders. For example, enhanced inter-hemispheric connectivity has been reported in children with attention deficit/hyperactivity disorder (ADHD) (Brown & Vickers, 2004; Chen et al., 2021; Mohamed et al., 2015; Roessner et al., 2004), and abnormalities in inter-hemispheric transfer times have been observed in adult ADHD patients (Rolfe et al., 2007). Furthermore, previous studies in stroke patients with spatial neglect support an association between behavioral performance and inter-hemispheric, but not intra-hemispheric, FC between homologous brain regions (Baldassarre et al., 2016; Carter et al., 2010; He et al., 2007; Siegel et al., 2016; Veldsman et al., 2017).

In the present work, we sought to examine the relationship between intra/inter-hemispheric functional connectivity and behavioral performance in a sustained visuo-spatial attention task by analyzing the correlations of the blood oxygenation level-dependent (BOLD) signal time series measured by steady-state functional magnetic resonance imaging (fMRI). We used a-priori whole-cortex region of interest (ROI) and network functional parcellation based on independent data from the Brain Genomics Superstruct Project (Hollinshead et al., 2015; Schaefer et al., 2018) to determine the relation between FC and behavioral performance in a cohort of healthy subjects during a covert (i.e., gaze-independent) visuospatial attention task designed to isolate the effect of the attended side (attention to left vs. attention to right).

2 | METHODS

2.1 | Subjects

Fifteen healthy subjects (Table 1) gave informed written consent to participate in this study, according to the Helsinki declaration and to European Union regulations. The study was carried out following a protocol approved by the local Ethics Committee. Exclusion criteria included any known vascular and neurological disease. All participants had normal or corrected-to-normal vision, and all except three were right-handed. To account for sample variability, the hand preference, sex, and age were used as nuisance covariates (see also below) in all statistical analyses.

2.2 | Spatial bias and ocular dominance

To evaluate spatial bias, study participants were asked to perform the line bisection task, generally used to evaluate attentional impairments

Subject	Age (years)	Sex (M/F)	Handedness (L/R)	Dominant eye (L/R)	Spatial bias
1	18	F	R	L	−0.13
2	28	M	R	R	−0.10
3	44	M	R	R	n.d
4	24	M	R	R	n.d
5	23	M	R	R	−0.10
6	24	F	R	R	−0.05
7	27	M	R	R	0.10
8	22	F	R	R	0.00
9	21	M	R	L	0.30
10	24	F	R	R	0.16
11	23	M	L	R	−0.17
12	24	F	R	L	n.d
13	24	M	L	R	−0.20
14	31	M	L	L	−0.20
15	24	F	R	R	0.25
Average	25 ± 6	9M, 6F	12R, 3L	10R, 5L	−0.01 ± 0.05

TABLE 1 Study subjects

in neurological patients (Molenberghs & Sale, 2011). A side underestimation has been traditionally associated with a contralateral hemisphere dominance for spatial attention. Although bisection errors could be possibly attributed to a lack of awareness of the left end-point (Kinsbourne, 1993), we complied with standard measurements in the field, and did not perform, for instance, end-pointing weightings bias (EWB), as suggested elsewhere (McIntosh et al., 2017). Furthermore, since psychometric studies suggest a relationship between the sighting ocular dominance and shifts of spatial attention (Shneur & Hochstein, 2006, 2008), the dominant eye was identified for each participant using a variation of the hole-in-the-card test. Ocular dominance was used as an additional nuisance covariate (see above) in all statistical analyses.

2.3 | MRI acquisitions

MRI data were acquired on a 3 T MRI Scanner (Siemens, Magnetom Allegra) equipped with a standard birdcage coil. BOLD-weighted images were collected during a steady-state visuospatial attention task using a multi-echo planar image sequence (Speck & Hennig, 1998) (TR = 3100 ms, TE1/TE2/TE3 = 16, 39, 63 ms, Flip Angle = 85°, voxel size = $3 \times 3 \times 3.75 \text{ mm}^3$, FOV = $192 \times 192 \text{ mm}^2$). Two runs were acquired for each subject, with attention either to the left or to the right hemifield. Each run, composed of 246 volumes (including four dummy scans), lasted 12 min and 43 s. Clinical images were also collected to exclude any pathological condition and to comply with institutional guidelines.

2.4 | Stimulation and task

Functional scans were collected while subjects performed a covert attention motion-detection task. The visual stimulus consisted of two bilateral circle-shaped (3° of radius) white-black rotating (2 cycles/s) checkerboards positioned in the left and right hemifield at 4° of horizontal from the central fixation point, with a uniform gray background (see Figure 1a). The checkerboards were simultaneously and continuously present on both the left and right sides of the screen. The two checkerboards inverted the rotation direction, independently of one another, at variable intervals (with period uniformly distributed between 1 and 3 s; average 2 s). A white arrow at the center of the screen indicated the relevant side/checkerboards and also served as the fixation point. The relevant side was attended for the entire duration of the fMRI run. The subjects were instructed to covertly attend the relevant side (i.e., without shifting gaze from the central arrow), and to push an MRI-compatible button for every change in the direction of rotation of the relevant checkerboard. Two functional runs were acquired, with cued attention either to the left or to the right checkerboard; the acquisition order was randomized between subjects. The visual stimulation was delivered during functional scans using a Digital Light Processing (DLP) projector located outside the MR scanner room and projecting the stimulus on a screen positioned

on the magnet bore. The subjects viewed the stimulus projected behind them via a mirror fixed to the head coil. The two conditions (attention to left and attention to right) are compared relative to each other, while we avoided a third condition (for instance, attention to center) because it would have introduced a substantial difference in the task difficulty as well as in the type of judged visual feature (i.e., we are detecting responses to changes in the rotation of the fixation cross, which is located in the center of the visual field). Moreover, a third condition would have been inconsistent with the focus of our study, which is covert attention (i.e., away from fixation). Since covert attention guided the design of the current experiments, any other condition of directed attention would have removed such implicit selection process.

2.5 | Subject behavior

The subject's gaze was monitored during the functional scans through an eye-tracking system (Applied Science Laboratories, model 504) equipped with a remote pan/tilt optic infrared module and a video camera that was custom-adapted for use in the scanner. In-scanner telemetry and nine-point calibration were performed for each subject using the eye-tracker interface software. All signal traces were linearly interpolated and smoothed (after an up-sampling to 1 kHz) by a box-car filter (width $\pm 25 \text{ ms}$). To correct for motion shifts, motion parameters from the corresponding fMRI series were regressed out from signal time courses. Gaze position averages (1 s-wide) were computed to evaluate any systematic gaze shifts time-locked to the target presentation. The fulfillment of the central fixation task was confirmed by both online and offline performance check (see Figure 1a–d). Subject's performance during the steady-state task was assessed by means of reaction times (RT) and error rate recording. Subject's responses were considered valid if falling inside a 700 ms window after target onset (fast responses, e.g., $<150 \text{ ms}$, were $<1\%$ of the total).

2.6 | Image processing

Functional images were preprocessed with AFNI (Cox, 1996). After discarding four dummy scans, head-motion parameters were estimated from the second-echo series using the first volume as reference (3dvolreg). Each echo series was compensated for systematic slice-dependent time shifts (3dTshift) and then motion corrected by applying the previously estimated transformation matrices (3dAllineate). Non-brain regions were removed with 3dAutomask. The three-echo series were cleaned from spurious signals using the multi-echo ICA denoising (Kundu et al., 2012; Kundu et al., 2013) implemented in “tedana.py,” which also combined the three-echo series into a single cleaned series using a $T2^*$ -weighting average (Posse et al., 1999). Images were then normalized to Montreal Neurological Institute (MNI) space ($3 \times 3 \times 3 \text{ mm}^3$) using as source image the mean of the motion-corrected second-echo series and by

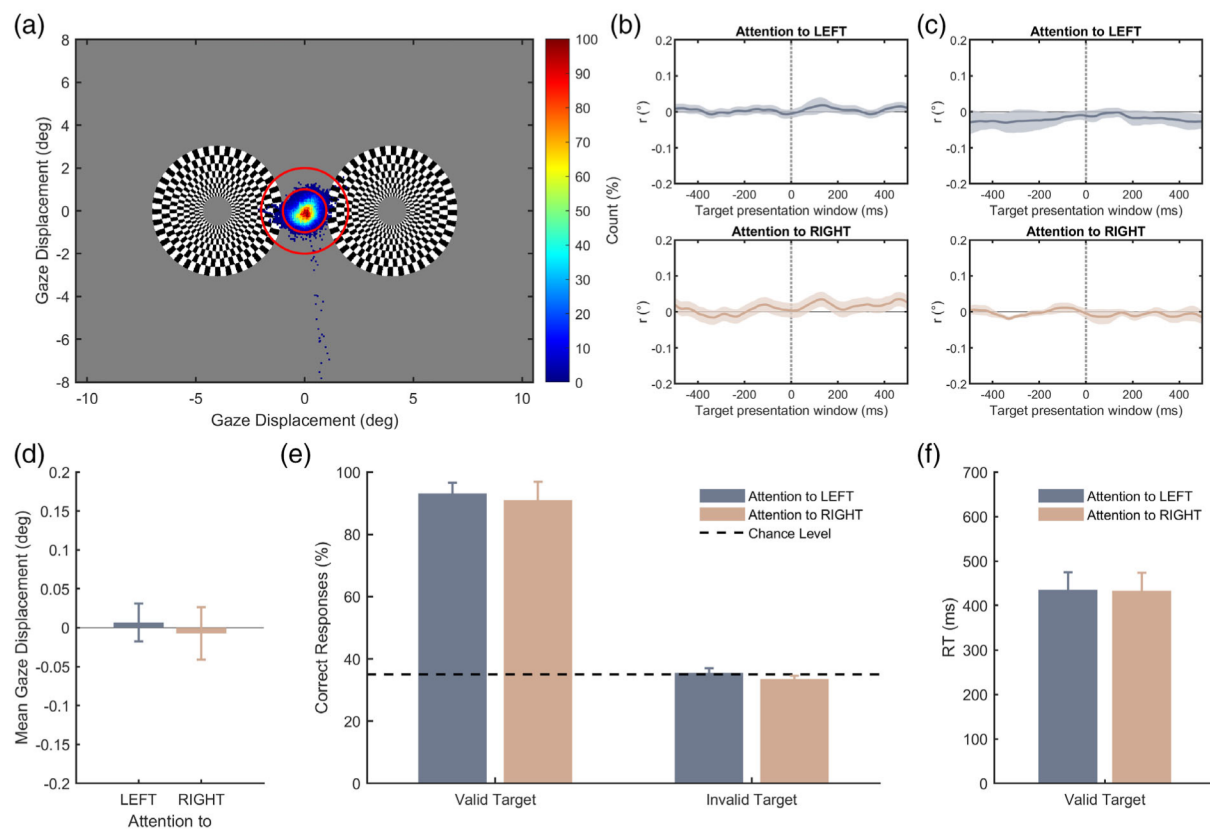


FIGURE 1 Eye movements recording and group-level behavioral data. (a) Eye positions overlapped onto the visual stimulation for one representative subject during the covert attention to the left checkerboard. Red circles mark points, whose distance from the central fixation arrow (not visible) is less than one or two visual degrees. Almost all points fell into the first circle. (b) Eye movements, expressed as the distance from the central arrow, during the target presentation window for one representative subject and (c) the corresponding average across subjects. The vertical gray line marks the onset of rotation-direction change of the attended checkerboard. (d) Mean gaze displacement across subjects during the two attention conditions are not significantly different. (e) Group-level accuracy in detecting the motion of the attended (valid) and not attended (invalid) target (i.e., checkerboard). As expected, accuracy level for the invalid target was consistent with the chance level (35%, corresponding to the ratio between response window and average checkerboard rotation period). (f) Group-level RT in detecting the motion of the attended target. No attention direction effect (i.e., leftward or rightward) was reported for motion detection of the valid target, neither in the accuracy nor in the RT measure

concatenating (3dNwarpApply) a linear (@auto_tlrc) and a nonlinear transformation (3dQwarp). The recorded time-courses of each subject's response times (time-locked to keypresses; duration = 0) were convolved with the canonical hemodynamic response function of the SPM package (<http://www.fil.ion.ucl.ac.uk/spm>) and used as confound regressors in the subsequent analysis. Nuisance signals, which included a Fourier basis accounting for low frequencies (<0.008 Hz), linear and quadratic trends, motion-derived parameters, as well as the first five principal components extracted from the cerebrospinal fluid and white matter compartments (Behzadi et al., 2007), were removed via linear regression, as previously described (Mascali et al., 2021). To correct for potential intensity inhomogeneities across the brain, a bias field correction was applied. The bias field map was estimated with the segmentation routine (Ashburner & Friston, 2005) of SPM on the mean series. Finally, images were smoothed within the brain mask with an isotropic 8 mm FWHM Gaussian Kernel (3dBlurInMask). It is noted that our choice of delivering a continuous (i.e., steady-state) stimulation allowed us to avoid regressing out task-evoked activity

signals from fMRI time-series, which can be cumbersome and lead to spurious correlations (Gonzalez-Castillo & Bandettini, 2018). We also avoided the sampling of the transients at stimulation onset with dummy scans (corresponding to 12.4 s at the beginning of each session). Furthermore, the rate of target presentation (0.33–1 Hz) was above the Nyquist frequency (0.16 Hz) associated with the determination of FC.

2.7 | Regions of interest and network-based connectivity

Whole-cortex average network to network connectivity analysis was performed using a parcellation approach. Specifically, independent resting-state fMRI atlas data in MNI space were functionally parceled into 400 ROIs (200 for each hemisphere) according to a gradient-weighted Markov Random Field model integrating local gradient and global similarity approaches (Schaefer et al., 2018). The 400 parcels

were classified according to a maximum overlap criterion into one of seven standard networks, namely visual (VIS), sensorimotor (SMN), dorsal attention (DAN), ventral attention (VAN), limbic (LIM), frontoparietal (FPN), and default mode (DMN) networks (Yeo et al., 2011; Figure S1).

Connectivity between each couple of ROIs or networks in each subject was evaluated in two steps. First, Pearson's correlation was calculated between couples of time series averaged across voxels within each ROI (for the ROI-based analysis), and across ROIs within each network (for the network-based analysis). Second, functional connectivity between couples of either ROIs or networks was calculated by averaging the z-transformed correlation coefficients between either voxels or ROIs, respectively. Such approach is intermediate between averaging the connectivity between each couple of voxels within the whole networks, and averaging the time courses within the whole networks and then calculating the correlation, and is expected to better preserve the homogeneous properties of each ROI (Craddock et al., 2012). Hemispheric functional segregation was expressed in terms of the average strength of intra-hemispheric FC (i.e., between-hemispheres connectivity) relative to the average strength of inter-hemispheric FC (i.e., within-hemispheres connectivity) (Cohen & D'Esposito, 2016). Conforming to previous work (Chan et al., 2014), we defined the segregation index (SI) for a set of ROIs or networks (eventually separated in different hemispheres) as $SI = (1 - \langle Z_B \rangle / \langle Z_W \rangle)$, where $\langle Z \rangle$ is the Fisher z-transformed FC averaged between (B) or within (W) the corresponding ROIs or networks.

2.8 | Statistics

Partial correlation coefficients were calculated after adjustment for internal variables (as nuisance covariates: age, sex, handedness, dominant eye). Where relevant, paired-sample t-tests were corrected for multiple comparisons using False Discovery Rate (FDR). To account for the small sample size, least-square regressions were compared with robust regressions using the Huber fitting weight function (Huber, 1981). To further account for inter-subject variability, we calculated the Bayes factor (BF) for hypothesis testing as well as for Pearson correlation (Nuzzo, 2017). Unless otherwise stated, all results are given as mean $\pm$ SD.

3 | RESULTS

3.1 | Covert visual attention task

Eye movement analysis confirmed that subjects were able to maintain the gaze on the central fixation arrow. The average eye fixation point around target presentation shows a consistent eye position (Figure 1a,b), which across subjects was not significantly (paired t-test 500 ms before vs. 500 ms after; $p = .40$ for attention to left, $p = .51$ for attention to right) affected by the target onset

(Figure 1c,d), that is, the change in rotation direction of the attended checkerboard.

3.2 | Individual task performance

The group-average accuracy level for target discrimination was around 90% for covert attention to both left and right (Figure 1e). Subjects reported no difficulty in performing the task for either condition (i.e., attended sides). Accordingly, direction of attention, leftwards or rightwards, did not affect the accuracy level nor the RT (paired t-tests; $p = .38$ and $p = .82$, respectively) (Figure 1e,f). Similarly, we found no significant spatial bias (one-sample one-tailed t-test, $p = .41$; see Table 1), probably due to the ease and/or lack of sensitivity of this test (see, e.g., Benwell et al., 2014).

3.3 | ROI-to-ROI connectivity

The patterns of FC among the different ROIs appear to be similar (correlation coefficient of the FC matrices, $r = .98$, $p = 0$) during attention to left and attention to right (Figure 2a,b; see also Figure 4 below). Similarly, we found that average FC strength was not significantly (one-way ANOVA, $F = 0.53$, $p = .75$) lateralized in the two conditions (Figure 2c,d). Notably, hemispheric SI was statistically significant (i.e., greater than zero) under both attention to left ($SI = 0.09 \pm 0.03$, one-sample t-test, $p < .0001$, $BF = 24.8$, very strong evidence) and attention to right ($SI = 0.11 \pm 0.05$, one-sample t-test, $p < .0001$, $BF = 19.1$, very strong evidence), with no difference between conditions (paired t-test, $p = .26$, $BF = 0.4$, no evidence) (Figure 2c,d). Analysis of the FC difference showed that the set of regions exhibiting high FC is distinct during the two conditions (Figure 2e,f). The distributions of the FC in the two conditions are significantly different, with more (less) connections in the right (left) tail of the distribution, which entails larger FC within and between hemispheres during attention to left than during attention to right (Figure 2g,h).

3.4 | Network-to-network connectivity

When restricting the analysis of the FC strength to the ROIs in the VIS network, we found that the only significant results were those involving the right visual areas, with FC being larger (R_{VIS-L} , paired t-test, $q_{FDR} = 0.0189$, $BF = 10.4$, strong evidence; R_{VIS-R} , paired t-test, $q_{FDR} = 0.0055$, $BF = 29.6$, strong evidence) during attention to left compared with attention to right (Figure 3a). Analysis of FC differences confirmed that the major difference between the two conditions was the FC of the right visual network during attention to left (Figure 3b,c). In particular, only the connections of the right visual network with bilateral DAN (one-sample t-test, right DAN: $q_{FDR} = 0.0375$, $BF = 4.6$, moderate evidence; left DAN: $q_{FDR} = 0.0148$, $BF = 10.1$, strong evidence) and with bilateral VAN (one-sample t-test, right VAN: $q_{FDR} = 0.0010$, $BF = 96.9$, very strong

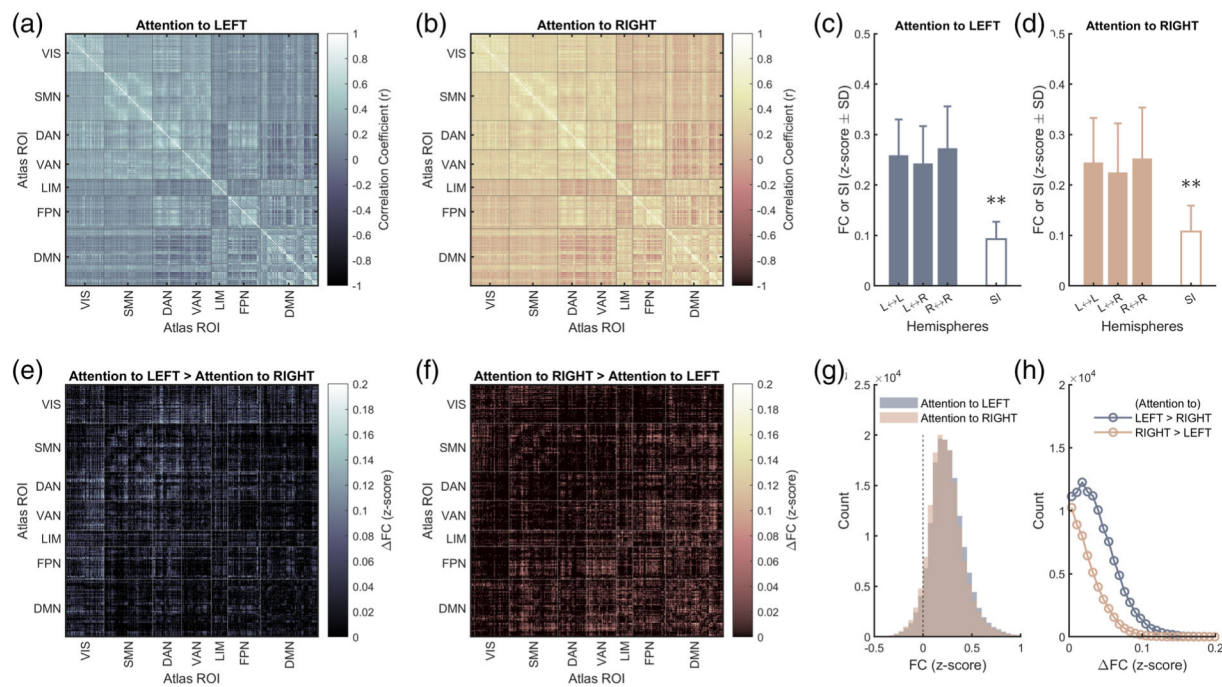


FIGURE 2 (a,b) correlation matrices during attention to left (a) and attention to right (b) underlie similar averaged intra/inter-hemispheric FC patterns as well as statistically significant (** $p < .001$) positive hemispheric functional segregation index SI c,d; see text). (e,f) difference matrices (ΔFC) exhibit asymmetric ROI-to-ROI connectivity, with different networks recruited during attention to left (e) compared with attention to right (f), as further evidenced by the distribution of the FC (g) and ΔFC (h) values for the two conditions

evidence; left VAN: $q_{FDR} = 0.0011$, $BF = 89.9$, very strong evidence) during attention to left survived correction for multiple comparisons, while nothing was significant ($q_{FDR} > .3$) during attention to right (Figure 3b,c insets).

Although the FC strength varied across conditions (see above), the topology of the connections was clearly maintained. Incremental threshold analysis showed the same FC patterns during attention to left and attention to right (Figure 4a,b,c). Accordingly, the average z-transformed correlation matrices were not significantly different (paired t -test; $p = .8$, $BF = 0.2$, no evidence) for the two conditions (Figure 4d,e,f).

3.5 | Correlation between functional segregation and task performance

We found no significant correlation between SI and the percentage of correct responses ($q_{FDR} > 0.05$; data not shown). On average, the correlation matrices between SI and RT revealed distinct qualitative patterns of intra-hemispheric and inter-hemispheric connections (Figure 5a,b), that however did not result in any significant difference (one-way ANOVA, $F = 1.37$, $p = .23$) for the two conditions at the whole-hemisphere level (Figure 5c). On the contrary, we found significant positive correlations between SI and RT between individual networks of opposite hemispheres (Figure 5d,e,f). In particular, the RT decreased with increasing SI between left VIS and right VIS ($r = -.47$, $q_{FDR} = .0142$), left DAN and right DAN ($r = -.52$, $q_{FDR} = .0057$), as

well as left DAN and right VAN ($r = -.50$, $q_{FDR} = .0077$). Notably, the absolute values of the correlation coefficients showed a trend to be higher (i.e., steeper slopes) during attention to right than during attention to left, although that was not statistically significant ($p > .1683$). Robust regression confirmed significant correlations for VIS-VIS ($q_{FDR} = 0.0065$), DAN-DAN ($q_{FDR} = 0.0020$), and DAN-VAN ($q_{FDR} = 0.0001$). Bayes Pearson correlation analysis yielded moderate evidence for VIS-VIS ($BF = 3.95$, $r = -.47$, $p = .0095$) and DAN-VAN ($BF = 5.95$, $r = -.49$, $p = .0060$), as well as strong evidence for DAN-DAN ($BF = 12.47$, $r = -.53$, $p = .0026$). No significant correlation was found between any pair of intra-hemispheric networks ($q_{FDR} > 0.05$; data not shown). Finally, no significant correlation was found between either FC, SI, or task performance and spatial bias ($q_{FDR} > .41$, $q_{FDR} > .28$, and $p > .27$, respectively; data not shown).

4 | DISCUSSION

In this study, we characterized the effect of sustained visuospatial attention on steady-state FC. The direction of attention induced a modulation of connections between brain networks, with attention to left involving regions in the VIS, SMN, and DAN networks, while attention to right involving regions in the VAN, LIM, FPN, and DMN. The reorganization involved specific modulations of connectivity strength but did not otherwise alter the overall topology of the networks (Figures 2a,b and 4). The modulation of the connectivity strength was primarily due to the connections of the right visual

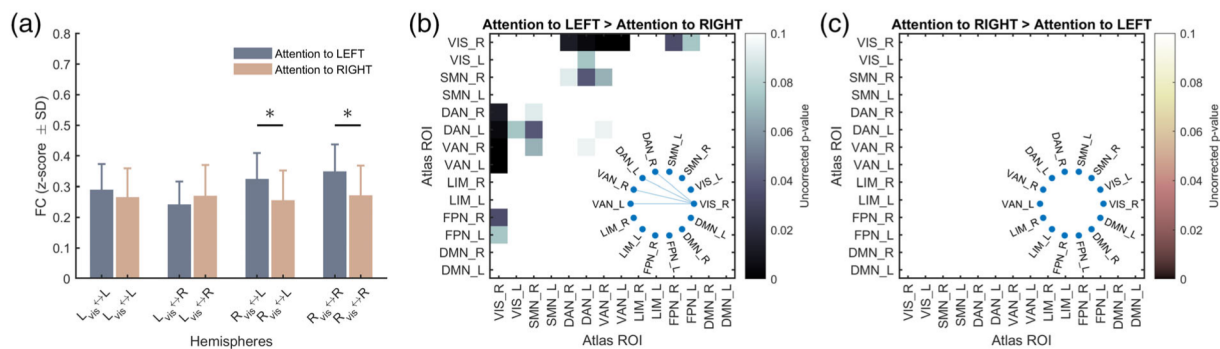


FIGURE 3 (a) Intra- and inter-hemispheric FC calculated on the visual network (VIS) seed confirms the asymmetric patterns and reveal a predominant role of the right visual network during attention to left compared with attention to right, that is, $R_{vis} \leftrightarrow L$ and $R_{vis} \leftrightarrow R$ individually different ($*q_{FDR} < .05$) across the two conditions (see text). (b,c) similarly, the statistically significant differences in connectivity (ΔFC) are restricted to the connections between right visual network and bihemispheric VAN and DAN only during attention to left (b), while no connectivity difference is significant during attention to right (c)

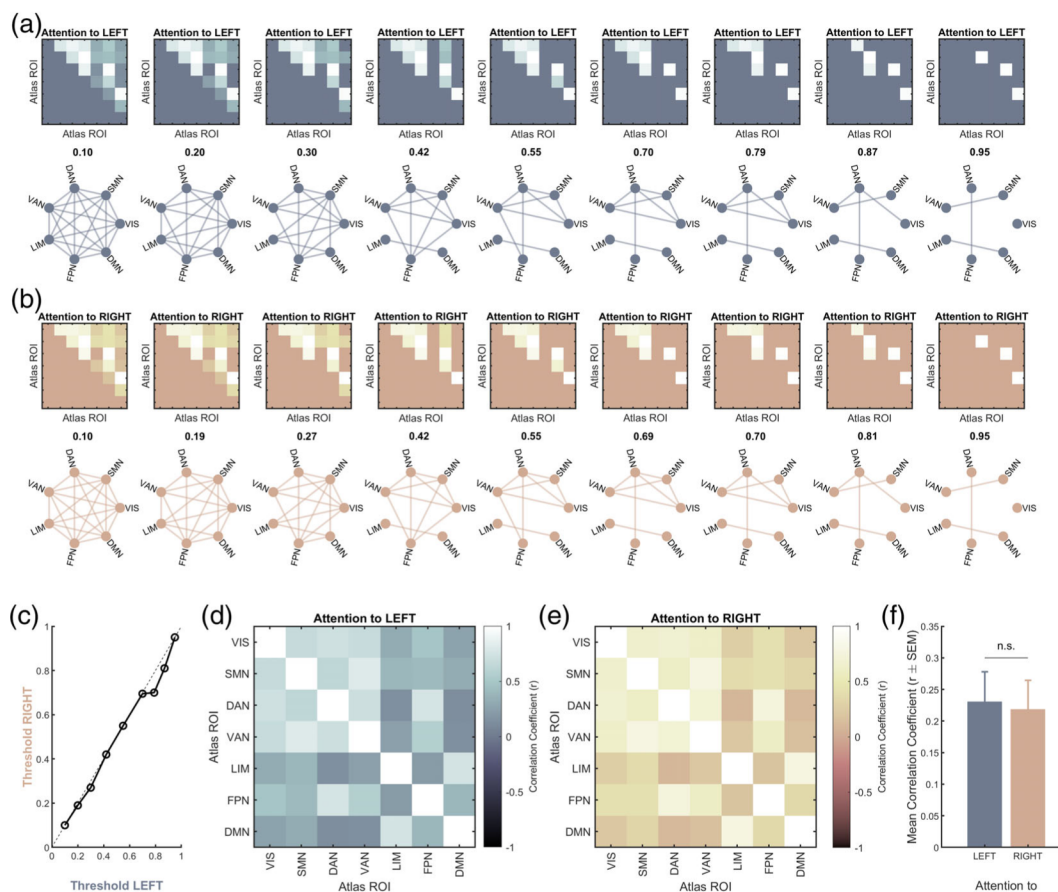


FIGURE 4 (a,b) Incremental threshold (i.e., inverse of the density of connections, with zero corresponding to the fully connected graph) for the conversion of correlation matrices to adjacency matrices shows strikingly similar patterns for attention to left (a) and attention to right (b), with slightly lower thresholds for the latter condition (c, as expected due the overall higher FC strength during attention to left). (d,e) The similar organization of the FC patterns is confirmed by the network-to-network correlation matrices during attention to left (d) and attention to right (e), whose average is not significantly different (f)

network with both the left and right hemisphere (Figures 2c–h and 3), in keeping with the fact that the right hemisphere is more active during visuospatial tasks (Cavérian et al., 2012; Çiçek et al., 2009; Fink et al., 2000; Fink et al., 2001; Foxe et al., 2003; Longo et al., 2015).

The asymmetry in visuospatial attention arises early in development (Yaakoby-Rotem & Geva, 2014) as a result of several complex interactions between genetic and ontogenetic factors (Güntürkün & Ocklenburg, 2017; Schaafsma et al., 2009) as well as non-genetic

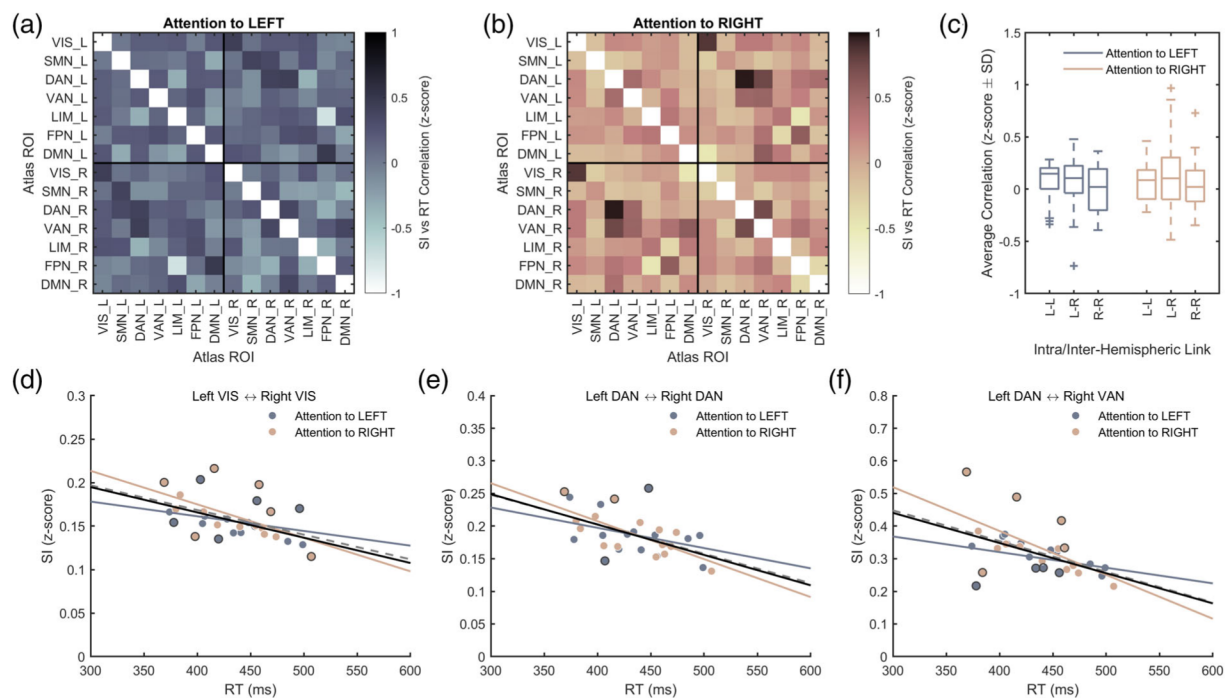


FIGURE 5 Group-level correlations between functional segregation and behavioral data. (a–c) Globally, SI exhibits very similar correlation patterns with RT during attention to right and during attention to left. (d–f) At the individual network level, RT is negatively correlated with SI for networks of the left and right hemisphere (i.e., with inter-hemispheric connections), namely VIS–VIS (d), DAN–DAN (e), and DAN–VAN (f). Analysis of outliers (gray-circled data points) performed using robust regressions (black lines) confirmed the significant correlations obtained using least square regressions (dashed dark gray lines). Behind the significant correlations of the pooled data sets, there is a non-significant tendency for the effect to be stronger during attention to right than during attention to left

mechanisms such as biomechanical bias (e.g., handedness) and visual scanning bias (e.g., due to cultural habits associated with reading and writing practices) (see, e.g., Mendonça et al., 2020; Rinaldi et al., 2020). Adult neurologically normal human individuals commonly exhibit a right hemisphere dominance in the control of visuospatial attention (Bowers & Heilman, 1980; Jewell & McCourt, 2000). Notably, we did not find any tendency to over-attend the left side of the space, as evidenced by a similar number of correct responses and RT in the two conditions, much likely because of task simplicity (Figure 1e,f; see below). However, we found that several connectivity changes were behaviorally relevant, with task performance being strongly correlated with the degree of segregation between specific areas of the two hemispheres, even in the presence of functional asymmetries (Figure 5). It is commonly observed that inter-hemispheric FC determined during resting wakefulness is positively correlated with subsequent behavioral output during a task (e.g., Carter et al., 2010). Yet, how inter-hemispheric FC determined during the execution of a task (here, sustained selective visuospatial attention) affects performance has not been investigated, and according to our results such correlation is negative in several specific brain networks (see Figure S2).

The two hemispheres can both attend left and right hemifields due to inter-hemispheric transfer of information from the contralateral to the ipsilateral hemisphere, possibly mediated by subcortical structures (e.g., brainstem/midbrain nuclei) and/or white-matter

(e.g., transcallosal) fibers. Whether the inter-hemispheric connectivity is inhibitory or facilitatory to the attentive process is an object of debate (Siman-Tov et al., 2007 and references therein). Although the present study cannot shed light on the mechanism of inter-hemispheric communication, our results are largely consistent with the hemispatial theory (Mesulam, 1981, 1999) as well as with the hemispheric rivalry model (Kinsbourne, 1977; Valero-Cabré et al., 2020). In particular, there is a clear asymmetry in the connections that the right visual network maintains with the rest of the brain (in both hemispheres). These connections are stronger during attention to left than attention to right, confirming the dominant role of the right hemisphere in attentive mechanisms. During attention to right, it is the left hemisphere to receive and process the information that eventually needs to be transferred to the dominant right hemisphere (where the right visual network plays a major role, see above). Such inter-hemispheric transfer is possibly analogous to what happens to the language-dominant left hemisphere during split visual field experiments (Doron et al., 2012). Importantly, the FC between the dominant and non-dominant hemispheres that we report here is not restricted to the sensory (i.e., visual) network, but involves also the dorsal/ventral attention networks, likely explaining the ensuing rise in task RT. Although the optimal performance is associated with low inter-hemispheric FC, the right hemisphere appears to be engaged in both leftward (directly) and rightward (indirectly) attention, consistent with the hemispatial theory. Moreover, the degree of connectivity

between hemispheres is detrimental for performance, consistent with the hemispheric rivalry model.

Under the conditions of the present study, the lateralization of FC during visuospatial attention does not translate to a lateralization of task performances, that is, we do not find better performance during attention to left, as it would have been expected based on the literature. Similarly, we did not observe a significant spatial bias, that is, a measure of pseudo-neglect (Table 1), which possibly explains why there was no correlation between spatial bias and either FC or behavioral performance. In fact, the relation between functional segregation and target detection response time that we report here might well be dependent on task difficulty. Moreover, the relation might also be region-dependent, whereby cross-hemispheric collaboration and segregation are equally important (see, e.g., Davis & Cabeza, 2015). Finally, the impact of hemispheric segregation on performance could be modality-dependent. For instance, language processing can benefit of connectivity between hemispheres under certain experimental conditions, which might reflect the distinct forms of left (biased to interact more strongly within the same hemisphere) and right (biased to interact more strongly with both hemispheres) functional lateralization (see Gotts et al., 2013 and references therein). Unfortunately, the relatively small number of subjects in our study did not allow the exploration of these possibilities, and further research is required to examine how intra- and inter-hemispheric FC can affect RT in a task-, region-, and modality-dependent manner using a larger sample size.

In conclusion, our results confirm the lateralization of visual attention to the right hemisphere, extending previous literature by highlighting an asymmetry of connectivity, which is specifically evident in the connections of the right visual network. To our knowledge, our study is the first to show a significant correlation between task performance, in terms of RT during covert visuospatial attention, and the degree of functional segregation. Overall, our findings suggest that the dominance of the right hemisphere in visuospatial attention is associated with an hemispheric segregation of visual and attention networks that is beneficial for behavioral performance.

AUTHOR CONTRIBUTIONS

Federico Giove, Emiliano Macaluso, and Silvia Mangia conceptualized and designed research. Giorgia Bussu, Daniele Mascali, Marta Moraschi, and Federico Giove performed experiments. Mauro DiNuzzo, Daniele Mascali, and Maria Guidi analyzed data. Mauro DiNuzzo wrote the main manuscript text. Mauro DiNuzzo and Daniele Mascali prepared figures. All authors reviewed and approved the manuscript.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All data that support the findings of this study are available from the corresponding author upon signing a MTA that would include a list of authorized researchers and the commitment to not distribute further the materials. Commercial use of the raw data is not permitted.

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