


Research Article

Hemispheric co-lateralization of language and spatial attention reduces performance in dual-task

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ABSTRACT

Hemispheric specialization of different functions is proposed to confer evolutionary benefits, yet the behavioral impacts of lateralization and its cognitive and neural mechanisms remain unclear. This study investigated the effect of lateralization pattern between language and spatial attention on dual-task performance and its association with callosal connectivity. Functional lateralization was assessed using fMRI verbal fluency and landmark tasks, and interhemispheric connections were evaluated through diffusion-weighted imaging. The typical lateralization pattern enhanced overall performance and reduced interference in dual-task compared to the co-lateralized pattern (both functions lateralized to one hemisphere). However, no differences were observed between the mirrored pattern (right language dominance and left attention dominance) and the co-lateralized pattern. While callosal connectivity did not significantly differ among groups, a negative correlation was observed between the lateralization degree and callosal connectivity. Our findings partially support the functional crowding hypothesis and offer insights into neurocognitive mechanisms underlying functional reorganization after brain lesions.

1. Introduction

A hallmark of the human brain is its pronounced hemispheric asymmetry of many cognitive functions. The left hemisphere primarily controls language production (Malik-Moraleda et al., 2022), word recognition (Van der Haegen et al., 2012), and praxis (Vingerhoets et al., 2013), while the right hemisphere is predominantly responsible for spatial attention (Corbetta & Shulman, 2011), emotion processing (Gerrits et al., 2020b), and face recognition (Rossion & Lochy, 2021). This characteristic is observed not only in humans but across a wide range of animal species, suggesting that such hemisphere differences may provide evolutionary advantages (Güntürkün et al., 2020; Güntürkün & Ocklenburg, 2017; Vallortigara & Rogers, 2005). Despite this, whether and how human behavior benefits from functional lateralization still largely unknown.

Extensive research has explored the relationship between functional lateralization and cognitive performance, mainly focusing on individual functions, yet findings remain inconclusive. While some studies

suggested that greater lateralization was associated with enhanced speech perception (Hirnstein et al., 2014) and reading (Chiarello et al., 2009), others suggested an inverse relationship with spatial attention (Zago et al., 2017), word and face processing (Hirnstein et al., 2010), and verbal fluency (Bartha-doering et al., 2018). Furthermore, several studies reported no significant correlation (Mellet et al., 2014; Van der Haegen & Brysbaert, 2018). Regarding lateralization direction, some studies suggested that typical left lateralization benefited verbal learning (Cano-López et al., 2018) and vocabulary (Groen et al., 2012), whereas others reported no significant differences in verbal fluency (Knecht et al., 2001) or spatial attention (Gerrits et al., 2020c).

Beyond individual function lateralization, prior studies have explored how alterations in one function's laterality can influence other functions and their behavioral outcomes, with a particular focus on the interaction between language and spatial attention. Clinical observations show that early brain injuries to the left hemisphere often trigger compensation mechanisms in the right hemisphere, specifically in language functions (Kim et al., 2018; Strauss et al., 1990). Such

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compensation typically results in both language and spatial attention being managed by the same hemisphere, a pattern referred to as “function co-lateralization”. Despite the right hemisphere’s integrity, this reorganization is accompanied by pronounced visuospatial deficits (Kim et al., 2018; Lidzba et al., 2006; Strauss et al., 1990). The crowding hypothesis posits that these non-verbal deficits stem from competitive demands on limited neural resources within one hemisphere, resulting in interference effects between functions. Consequently, the more resilient language function impedes the original functions of the right hemisphere (Levy, 1969; Strauss et al., 1990). In healthy populations, most individuals with atypically right-lateralized language also exhibit atypically leftward spatial attention (Badzakova-Trajkov, Häberling, Roberts, & Corballis, 2010; Cai, der Haegen, & Brysbaert, 2013), a pattern referred to as “mirrored lateralization”. A comparison of spatial abilities between mirrored and typical lateralization patterns revealed no significant differences (Cai et al., 2013), indicating that a complementary pattern, where two functions are dominated by separate hemispheres, could provide similar processing efficiency irrespective of the individual function’s lateralization.

A shift in perspective from the lateralization of a single-function to the lateralization pattern of multiple functions within individuals provides deeper insights into their impact on human behavior (Bryden et al., 1983; Gerrits et al., 2020b; Quin-Conroy et al., 2024; Strauss et al., 1990; Vingerhoets, 2019). However, previous related studies have yielded mixed findings. Some studies indicated potential disadvantages of an atypical lateralization pattern. For instance, Vingerhoets et al. (2018) and Gerrits et al. (2020b) measured participants’ lateralization pattern across four to six functions using fMRI and assessed their cognitive abilities using a neuropsychological status battery. They observed that individuals with greater deviation from a typical lateralization pattern exhibited poorer overall cognitive performance. Conversely, other studies revealed no significant differences among groups with different lateralization patterns in spatial ability (Cai et al., 2013; Häberling et al., 2011), reading, vocabulary, or phonological memory (Groen et al., 2012).

Most previous studies assessed behavioral performance using general cognitive tests or single-function tasks. These designs failed to consider a crucial implicit assumption of the crowding hypothesis: interference is generated by online functional competition. Unlike the induced function crowding observed in early lesion cases, which were driven by ongoing neuroplasticity, the detection of potential interference effects in the healthy adult population requires more sophisticated methods. In particular, behavioral paradigms that engage two different functions simultaneously, termed dual-tasks, are essential for explicitly exploring how online interference occurs. A dual-task paradigm implemented by Vallortigara and Rogers (2005) offered an excellent reference. In their study, chicks were trained to peck alone (single forage task) or to simultaneously monitor a predator overhead (dual-task). Those with a typical lateralization pattern, developed by exposure to light during hatching, outperformed non-lateralized controls incubated in darkness. In addition, no significant differences were observed in the single forage task. The researchers explained this using the parallel processing hypothesis, which posits that the distinct lateralization of foraging and predator detection allows the hemispheres to function simultaneously, thus increasing the efficiency of processing multiple streams of information (Vallortigara & Rogers, 2005). This paradigm design can be utilized as a model for developing comparable studies in humans, where interference effects can be quantified by contrasting dual-task performance with that obtained in single-tasks context.

Despite the potential insights that could be gained by exploring the interference effects on how lateralization patterns affect behavior, human studies that have incorporated dual-task conditions remain limited. To our knowledge, only three studies have employed this approach, integrating the verbal fluency with other tasks such as driving (Lust et al., 2011b), landmark (Lust et al., 2011a), or mental rotation (Zickert et al., 2021) to measure the language production and spatial

ability simultaneously. Among these studies, Lust et al. (2011a) reported better performance and less interference for individuals with a typical lateralization pattern compared to those with an atypical pattern, which included both mirrored and co-lateralized patterns. In contrast, the other two studies found no significant group differences in behavioral interference (Lust et al., 2011b; Zickert et al., 2021).

Upon examining previously employed task designs, we have identified several key enhancements to optimize the efficacy of the dual-task paradigms. First, to validly assess dual cognitive processing, it is essential to use continuous stimuli presentation. The presentation of stimuli at fixed or varying frequencies in traditional spatial attention tasks tends to disrupt ongoing verbal fluency generation, introducing a confounding factor in internal interference. Second, using continuous rather than binary response measurements would enhance assessment quality, allow better monitoring, and prevent tasks from being too simplistic to differentiate performance. Third, previous studies on laterality patterns involving dual-task conditions relied on functional transcranial Doppler ultrasound to measure lateralization. However, this method is limited by its spatial resolution (Flöel et al., 2005). In contrast, fMRI provides greater spatial precision, enabling the evaluation of lateralization in specific core regions.

What is the underlying mechanism by which different patterns give rise to behavioral variability? The parallel processing hypothesis, which emphasizes the cooperation of multiple brain networks, posits that the typical pattern of strongly lateralized functions facilitates dual-task processing in a more independent and efficient way. When lateralized functions are crowded within one hemisphere, behavioral deficiencies may become evident. This raises the question of how these different patterns evolved. One potential mechanism is the (a)typical development of the corpus callosum, which has been considered as a crucial factor in establishing functional lateralization (Gazzaniga, 2000; Ringo et al., 1994). Previous studies have explored its connection with language lateralization (Hinkley et al., 2016; Josse et al., 2008; Karolis et al., 2019; Verhelst et al., 2021; Zhu et al., 2024), yielding mixed results. For instance, Hinkley et al. (2016) found individuals with abnormal development of the corpus callosum exhibited reduced language laterality, indicating a positive correlation between the two. Conversely, Karolis et al. (2019) revealed that the callosal connectivity was negatively correlated with functional laterality. To our knowledge, Häberling et al. (2011) is the only study to specifically examine the corpus callosum’s role in the lateralization patterns of language and spatial attention. The study reported that individuals with atypical lateralization patterns, particularly those with right-co-lateralized patterns, exhibited higher anisotropic diffusion in the posterior segments of the corpus callosum. However, the findings were limited by the small sample size of atypically lateralized subjects and reliance on tensor-based measurements, which were hindered by crossing fiber issues (Jeurissen et al., 2013).

It is important to note that the function pairs examined in this study belong to different systems. Language and visuospatial functions are typically regarded as independent subsystems in models such as working memory (Baddeley, 1992), which supports the operation of multiple streams of information. Crowding these functions within the same hemisphere could be disadvantageous. Conversely, when interdependent functions, such as subcomponents of language (e.g., speech production and word recognition), are located within one hemisphere, this proximity can enhance the efficiency of language networks through intra-hemispheric communication (Cai & Van der Haegen, 2015). Our study primarily focused on the former scenario.

Although atypical function lateralization is uncommon in the healthy population, left-handers exhibit a higher prevalence of atypical lateralization for both language (Knecht et al., 2000) and spatial attention (Petit et al., 2015), accompanied by greater heterogeneity. When these two functions are considered together, the atypical lateralization pattern, defined as the presence of at least one atypically lateralized function, occurs more frequently among left-handers (Gerrits, 2024).

This makes left-handers an optimal group for investigating the behavioral correlates of different lateralization patterns.

In this study, our primary objective is to investigate the behavioral outcomes of different lateralization patterns between language and spatial attention, and their association with the corpus callosum. We specifically recruited a group of pre-screened left-handers from our previous study (Zhu et al., 2024), ensuring the inclusion of participants with either atypical or typical lateralization patterns. Functional lateralization of language production and visuospatial attention was assessed using the verbal fluency and landmark tasks, respectively, during fMRI sessions. A dual-task paradigm integrating a continuous spatial trisection task with a verbal fluency task was used. These tasks were also performed individually to evaluate interference by contrasting single-task and dual-task performance. Diffusion data were collected to obtain the interhemispheric connectivity. We hypothesize that if lateralizing to different hemispheres benefits human behavior through parallel processing, individuals with either a typical or mirrored lateralization pattern will outperform those with a co-lateralization pattern in dual-task performance. Furthermore, we expect decreased performance in the dual-task compared to the single-task, and this reduction will be more pronounced in participants with a co-lateralization pattern due to the “crowding” of brain functions. Lastly, if the emergence of different lateralization patterns is influenced by the corpus callosum, we expect to observe significant differences in callosal connectivity across groups.

2. Materials and methods

2.1. Participants

Participants were initially recruited online using the Chinese version of the Edinburgh Handedness Inventory (Yang et al., 2018). Next, two visual half-field tasks were employed to identify individuals with right language dominance (Gerrits et al., 2020a; Van der Haegen et al., 2011). Finally, 98 participants were selected to undergo MRI sessions. For more details on participant screening, refer to our previous work (Zhu et al., 2024). Ten participants were excluded due to either unidentified shadows in anatomical images, excessive head movement or significant signal dropout in diffusion-weighted images. Consequently, 88 participants (36 males; mean age: 22.20 years, range: 18–34 years) with usable functional MRI data proceeded to further analysis. Of these, 45 agreed to undertake the behavioral tasks. Two were excluded for failing to follow instructions, resulting in a final sample of 43 participants (14 males; mean age: 23.12 years, range: 19–34 years) for the behavioral analysis. Individuals with left language dominance and right spatial attention dominance were classified as having the typical lateralization pattern ($N = 46$ with MRI data; $N = 16$ with both MRI and behavioral data). Those with right language and left spatial attention dominance were categorized as having a mirrored lateralization pattern ($N = 21/16$). Individuals who exhibited the same hemispheric dominance for both functions were grouped into the co-lateralization pattern ($N = 21/11$). Additionally, the definition of dominance direction can be found in Section 2.6. The three groups showed no significant differences in age, gender, or handedness, either among those with both MRI and behavioral data (Suppl. Table 1) or among those with only MRI data (Suppl. Table 2).

This study was approved by the Ethical Committee of the East China Normal University. All participants provided informed consent and self-reported no history of brain injury or psychiatric disorders.

2.2. fMRI tasks

2.2.1. Verbal fluency task

This task was used to determine language lateralization, which has been demonstrated to capture language-related activation with strong robustness (Bradshaw et al., 2017; Cai et al., 2013; Wang et al., 2019). It

comprised alternating Pinyin and baseline blocks, intermixed with rest blocks. In total, there were 10 blocks of each task condition and 20 rest blocks, each lasting 15 s. In the Pinyin blocks, participants were presented with a letter in the center of the screen and instructed to silently produce as many single-character words as possible starting with the letter. In the baseline blocks, participants were shown the symbol “” and instructed to repeat the non-lexical sound “bou”. They were asked to report the average number of words produced for each letter immediately after the scanning, and this was cross-checked with overt task performance to confirm compliance with the instructions.

2.2.2. Landmark task

This task was used to assess the lateralization of spatial attention (Cai et al., 2013; Gerrits et al., 2020b), a well-established paradigm for evaluating spatial neglect, with high reliability and validity (Jansen et al., 2004). It consisted of 6 touch blocks, 6 bisection blocks, and 6 rest blocks, each of which lasted 21.6 s. Each cycle consisted of alternating bisection and touch blocks, with a rest block following every two blocks. In each block, a 4-second instruction was presented first, followed by 12 trials of 1.6 s spatial stimulus presentation separated by a 200-ms fixation between trials. In the bisection block, a short vertical line was presented on a horizontal line, with the position of the vertical line around the center of the horizontal line varying by 2.5 %, 5 %, and 7.5 % to the left or right (half trials) and directly in the center (half trials). The participants had to determine whether the vertical line bisected the horizontal line. In the touch block, the same stimuli were presented, but in 50 % of the trials, the two lines did not make contact. Participants were asked to determine whether the two lines touched.

2.3. Behavioral paradigms

2.3.1. Single-tasks

The verbal fluency task (Fig. 1A) was also used to assess speech production ability. Each trial began with a fixation for 1500 ms, followed by a letter for 500 ms. Participants then had 15 s to overtly produce words when a blank appeared. They were instructed to avoid deliberate tone-switching, i.e., changing tones of the same pinyin to produce different words. With this strategy, it was difficult to decide whether they were producing just the sound or specific words. The task was divided into two sections with eight trials each.

To assess visuospatial attention, we developed the Continuous Spatial Trisection Task (CSTT, Fig. 1B), an adaptation of the landmark task. This involved two primary modifications aimed at facilitating the simultaneous and independent execution of dual-tasks. First, the presentation format of the vertical line was changed from a discrete sequence to a continuous flow, thus eliminating the disruption caused by rhythmic presentation on word generation response. Second, the participants' task was altered from spatial bisection to trisection judgement. This adjustment served three purposes: first, it prevented the strategic fixation of gaze at a particular position on the horizontal line, since the trisection points are less familiar. Second, it imposed a higher cognitive load, thereby promoting sustained spatial attention. Third, it allowed for the collection of more data points, which is crucial for monitoring the dual-task process.

The experimental procedure for the CSTT, as illustrated in Fig. 1B, began with a fixation cross for 2 s, followed by a static horizontal line intersected by a perpendicular vertical line. During each trial, the vertical line moved uniformly across the horizontal line in three phases: from left to right, right to left, and then back to right, with each phase lasting 5 s, totaling 15 s per cycle. Participants were required to rapidly and accurately press the “1” key at the moments when the vertical line crossed the one-third and two-thirds points along the horizontal line. The task was divided into two sections, each comprising eight trials, resulting in a total of 96 data points.

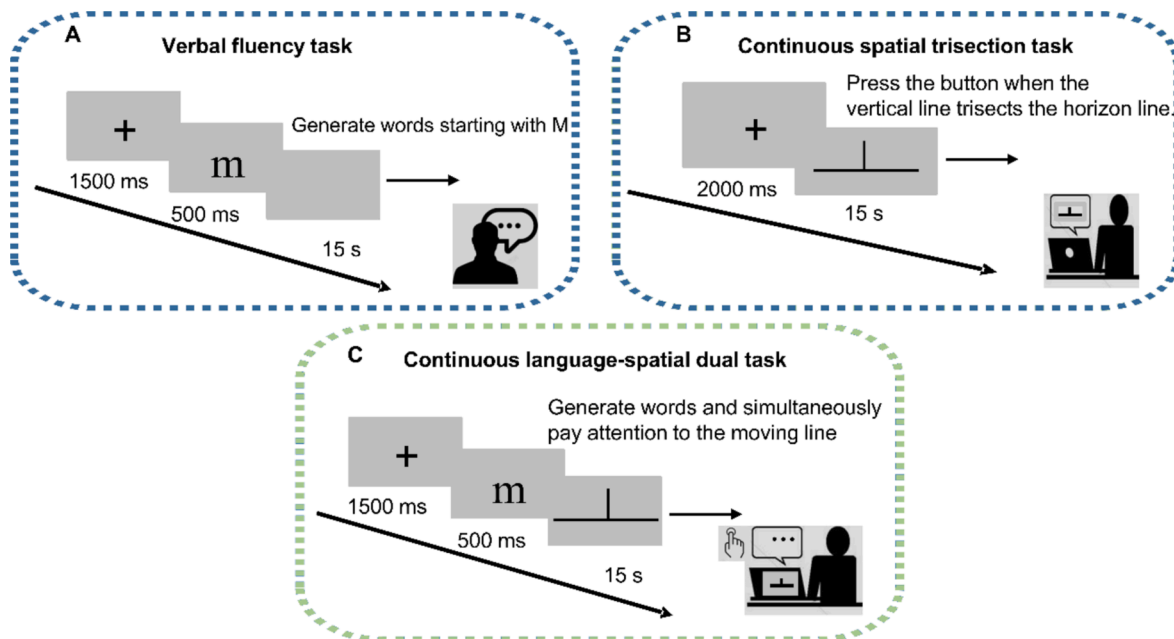


Fig. 1. Overview of the single- and dual-task paradigm. A) Single verbal fluency task. B) Single continuous spatial trisection task. C) Dual-task.

2.3.2. The continuous language-spatial attention dual-task

This dual-task integrated the two single-tasks (see Fig. 1C). Each trial began with a 1500 ms fixation, followed by a letter for 500 ms. Then, the two lines were displayed for 15 s. Participants were required to press a button when the vertical line trisected the horizontal line while simultaneously generating words. The task consisted of 16 trials, with a rest period incorporated halfway through.

The sequence of behavioral tasks throughout the experiment was as follows: participants first completed two single-tasks, each consisting of 8 trials. This was followed by the dual-task, after which the single-tasks were repeated. The order of the single-tasks was counterbalanced across participants to control for order effects. Prior to the formal experiment, participants performed one practice trial for each task. The same set of frequent letter stimuli was used for the verbal fluency task in both the dual-task and single-task conditions, reducing non-response trials associated with less frequent letters and facilitating a direct comparison of performance across both conditions. In addition, to investigate whether executive functions could potentially confound the attentional allocation during the dual-task, inhibitory control was measured using the stop-signal task. The procedure and calculation of measurements followed the guidelines in Verbruggen et al. (2019).

2.4. Behavioral data analysis

In the verbal fluency task, trials with no responses were excluded. These occurred in 0.6 % of dual-task trials involving three subjects with 5, 6, or 7 trials, respectively, and in others with fewer than four trials. Two participants who intentionally employed a tone-switching strategy were excluded from the analysis. The behavioral measure was the average number of words produced per trial. In the continuous spatial trisection task (CSTT), trials with missed keypresses were excluded. These occurred in 7.7 % of dual-tasks trials, primarily involving subjects with fewer than four trials (except one with seven trials) and in 1.4 % of single-task trials due to a data logging issue in one subject's run. The behavioral index, spatial bias, was calculated as the absolute difference between the time at which a keypress was made and the moment the vertical line reached the trisection position.

In the verbal fluency task, higher word counts reflected better performance, whereas in the spatial task, lower spatial bias denoted better performance. The overall dual-task performance was calculated by

subtracting the spatial task's z-score from the verbal fluency task's z-score, yielding an index where higher values correspond to better dual-task performance. The interference effect on language production was measured by subtracting the mean word count in the dual-task from that in the single-task. For spatial attention, the interference effect was measured by subtracting the spatial bias in the single-task from that in the dual-task. A higher value in both measures indicates a greater interference during the dual-task. Consequently, the overall interference was computed by summing the z-scores of both interference measures, with higher values indicating greater overall interference.

2.5. MRI acquisition

MRI data collection was conducted on a 3 T Siemens Prisma scanner equipped with a 20-channel head coil. T1-weighted images were obtained using an MPRAGE sequence (TR 2300 ms, TE 2.32 ms, voxel size $0.9 \times 0.9 \times 0.9 \text{ mm}^3$, FOV 240 mm, matrix size 256×256 , flip angle 9°). T2*-weighted images were acquired using an echo planar imaging (EPI) sequence (TR 2450 ms, TE 30 ms, FA 81° , matrix size 64×64 , FOV 192 mm, 40 axial slices, voxel size $3 \times 3 \times 3 \text{ mm}^3$).

Diffusion-weighted images (DWI) were obtained for 64 gradient directions using a single-shot EPI sequence with b values of 1000 (64 volumes) and 2000 s/mm^2 (64 volumes). Additionally, a pair of volumes with $b = 0$ and mirrored phase encoding directions was acquired. The corresponding parameters were as follows: TR 4200 ms, TE 70 ms, FOV 192 mm, voxel size $3 \times 3 \times 3 \text{ mm}^3$, matrix size 64×64 , 40 slices, FA 81° .

2.6. fMRI data analysis and the definition of lateralization patterns

Preprocessing of the functional MRI data was conducted with SPM12 (<https://www.fil.ion.ucl.ac.uk/spm/software/spm12/>), which involved several key steps, including slice-timing, spatial realignment, co-registration with individual anatomical images, normalization to MNI space, and Gaussian smoothing with a FWHM of 6 mm. Outlier volumes were identified using the ART toolbox (https://www.nitrc.org/projects/artifact_detect/) based on thresholds of motion $> 2 \text{ mm}$ or intensity deviations $> 4 \text{ SD}$. For each participant, condition-specific regressors were created by convolving onsets and durations with a canonical hemodynamic response function. These regressors were included in the general linear model along with motion and outlier parameters as

covariates.

Individual lateralization indices (LIs) were computed in specific regions of interest: the pars triangularis and pars opercularis for language production (Cai et al., 2013; Heim et al., 2008), and the inferior parietal lobe and the superior parietal lobe for spatial attention (Corbetta & Shulman, 2002). Symmetric masks of these regions were obtained by combining the original regions from the automated anatomical labeling atlas with their left–right reversals. LI computation was performed through a bootstrap method using the LI toolbox (Wilke & Lidzba, 2007). Participants were categorized based on LI signs of two functions, where a negative sign indicated right hemispheric dominance and a positive sign indicated left hemispheric dominance.

2.7. DWI preprocessing and tractography of the corpus callosum

The DWI data were processed in MRtrix3 (Tournier et al., 2019) using the recommended FBA pipeline (<https://mrtrix.readthedocs.io/en/latest/>). A fixel-based map of fiber density and cross-section was computed for each participant. The corpus callosum subdivisions were reconstructed using TractSeg (Wasserthal et al., 2018), with specific segments connecting the corresponding bilateral brain regions: the rostrum to the orbitofrontal areas, the genu to the prefrontal areas, the rostral body to the premotor areas, the anterior midbody to the motor areas, the posterior midbody to the postcentral areas, the isthmus to the superior temporal and posterior parietal lobules, and the splenium to the occipital and inferior temporal lobules. The mean combined fiber density and fiber-bundle cross-section (FDC) was computed for each tract and each participant. Detailed steps for data processing are outlined in Suppl. Material 1.

2.8. Statistical analysis

First, the distribution of the lateralization indices was examined using the Shapiro-Wilk test. A chi-square test was conducted to examine the independence between language lateralization and spatial attention lateralization. Second, given the non-normal distribution of our data, a series of Kruskal-Wallis tests were conducted to examine whether lateralization patterns (typical vs. mirrored vs. co-lateralization) were

associated with behavioral performance and interference effects between dual and single-tasks. To control the false discovery rate, post hoc adjustments for multiple comparisons were performed using Conover's test with Benjamini-Hochberg correction at a significance level of 0.05. Furthermore, lateralization patterns were re-defined by isolating the co-lateralization group and merging the mirrored and typical patterns into a complementary group. The association between these groups and behavioral performance was re-analyzed using the Wilcoxon test. Prior to this analysis, age, gender, and degree of lateralization were all regressed out as covariates of no interest. A similar analysis was performed to investigate the association between the lateralization pattern and the FDC of the corpus callosum subdivisions.

3. Results

3.1. The relationship between language hemispheric dominance and spatial attention dominance

The brain map of one representative participant from each group was shown in Fig. 2, depicting the activation of the frontoparietal language network and the dorsal attention network during the two single-tasks. The Shapiro-Wilk test revealed non-normal distributions for the lateralization indices of both language production ($median = 0.54$, $IQR = 1.17$; $W = 0.85$, $p < 0.001$) and visuospatial attention ($median = -0.54$, $IQR = 1.24$; $W = 0.86$, $p < 0.001$). The two functional LIs were distributed across the four quadrants (see Fig. 2). The chi-square test indicated a significant association between the directions of language lateralization and the visuospatial attention lateralization ($\chi^2(1, N = 88) = 17.73$, $p < 0.001$). Specifically, visuospatial attention was more likely to be left-lateralized when language production was right-lateralized. Of the 88 participants, 46 participants exhibited a typical lateralization pattern. Furthermore, 21 participants displayed a co-lateralization pattern, with 14 showing leftward and 7 showing rightward co-lateralization. The remaining 21 participants showed a mirrored lateralization pattern.

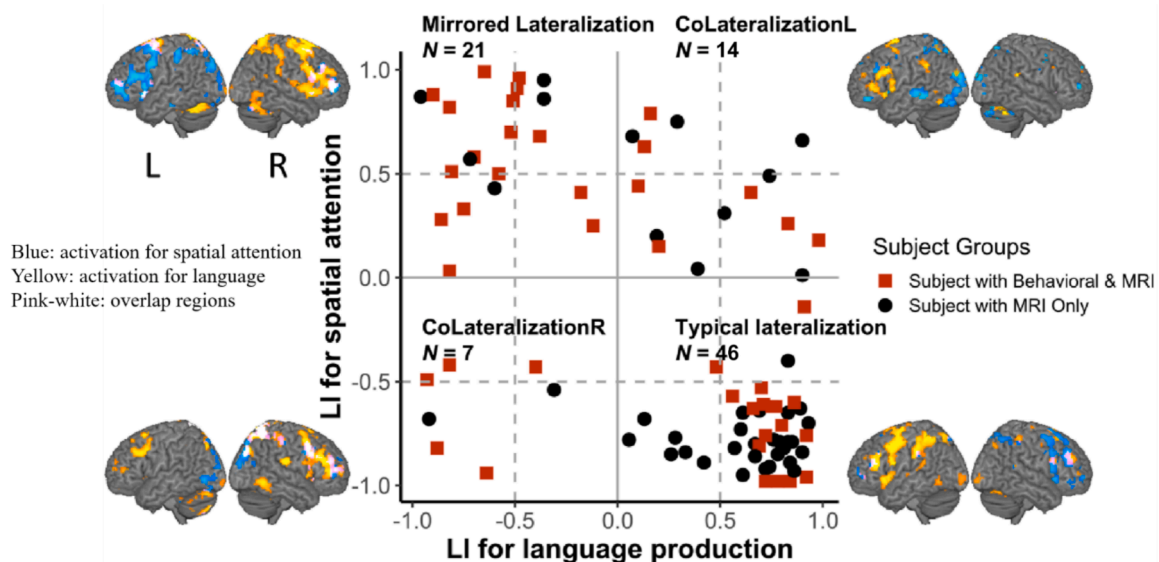


Fig. 2. The distribution of individuals with different lateralization patterns LI: lateralization indices, negative values denote right lateralization, while positive values denote left lateralization. Typical lateralization: left language dominance and right spatial attention dominance. Mirrored lateralization: right language dominance and left spatial attention dominance. CoLateralizationR: right language and right spatial attention dominance. CoLateralizationL: left language and left spatial attention dominance. Black circle: subjects who only had MRI data. Red square: subjects who had both MRI and behavioral data. The brain map during the two single-tasks of a representative participant from each lateralization pattern group was presented.

3.2. The effect of lateralization pattern on behavioral performance

For the single-tasks, Kruskal-Wallis tests indicated that there were no significant differences across groups in spatial bias in the continuous spatial trisection task ($\chi^2(2, N = 43) = 3.08, p = 0.214$, Fig. 3A), nor in the number of words generated in the verbal fluency task ($\chi^2(2, N = 43) = 1.07, p = 0.597$, Fig. 3B) after controlling for age, gender, and degree of lateralization. Furthermore, two lateralization patterns comparisons using the Wilcoxon tests revealed a marginally significant difference between groups in CSTT, where individuals with a co-lateralization

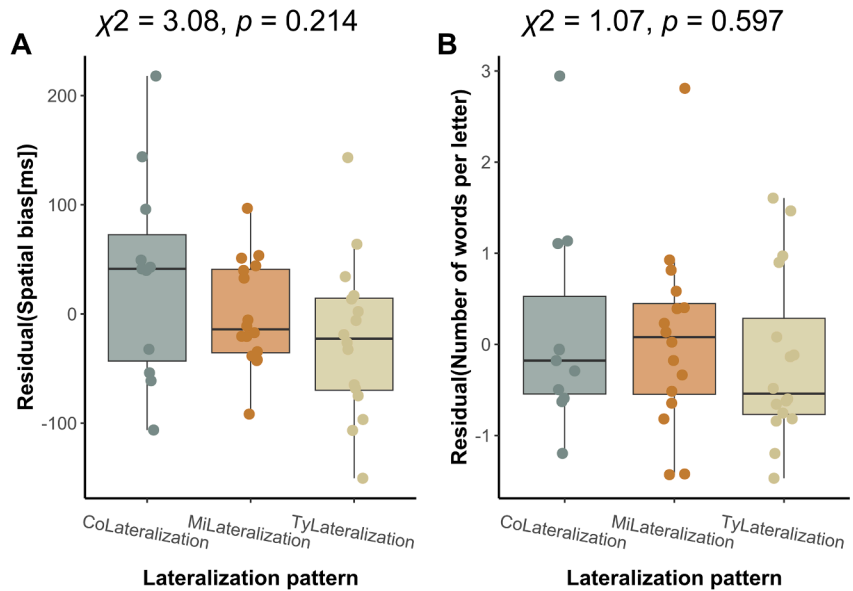
pattern (median = 41.4, IQR = 116) exhibited greater spatial bias compared to those with the complementary lateralization pattern (median = -18.1, IQR = 75.3; $W = 226, p = 0.085$, Suppl. Fig. 1A). No significant group differences were observed in the verbal fluency task ($W = 195, p = 0.704$, Suppl. Fig. 1B).

In the dual-task, the Kruskal-Wallis tests revealed a marginally significant effect of lateralization patterns on overall task performance ($\chi^2(2, N = 43) = 4.67, p = 0.097$, Fig. 3C) and a significant effect on the spatial bias ($\chi^2(2, N = 43) = 7.65, p = 0.022$, Fig. 3D) after controlling for age, gender, and degree of lateralization. However, no significant

Single-task

Continuous spatial trisection task

Verbal fluency task



Dual-task

Overall performance

Continuous spatial trisection task

Verbal fluency task

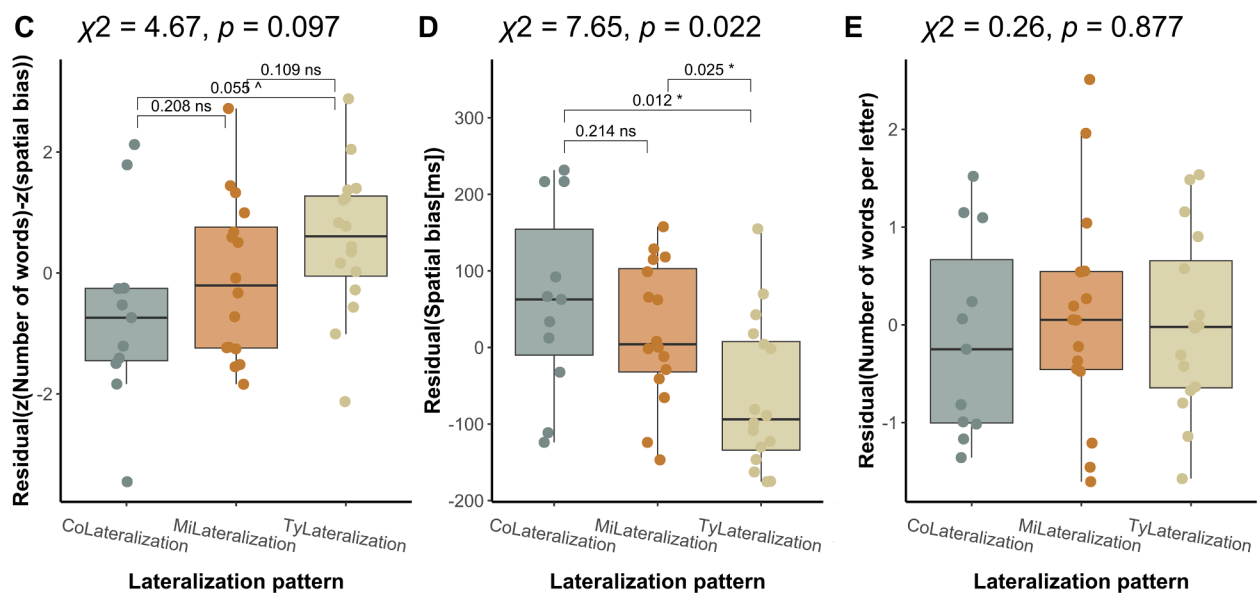


Fig. 3. Impact of lateralization patterns on task performance in single and dual-tasks. (A) No significant differences in spatial bias across groups in the single continuous spatial trisection task. (B) No significant group differences in number of words generated in the single verbal fluency task. (C) Individuals with a co-lateralization pattern showed lower overall dual-task performance compared to those with a typical lateralization group. (D) In the dual-task, individuals with a typical lateralization pattern displayed less spatial bias compared to the other two groups in the CSTT. (E) No significant differences among the groups in verbal fluency performance under dual-task context. Age, gender, and degree of lateralization were regressed out. Statistical significance is indicated by * for $p < 0.05$ and ^ for marginally significant. CoLateralization: same hemispheric dominance for both language and spatial attention. MiLateralization: right language dominance and left spatial attention dominance. TyLateralization: left language dominance and right spatial attention dominance.

effect was observed in the verbal fluency task ($\chi^2(2, N = 43) = 0.26, p = 0.88$, Fig. 3E). Post hoc analyses showed that individuals with a co-lateralization pattern ($median = -0.74, IQR = 1.20$) exhibited lower overall performance compared to the typical lateralization group ($median = 0.61, IQR = 1.32; T = -2.16, p = 0.055$) in dual-task, while other group comparisons yielded no significant differences ($ps > 0.05$). In the continuous spatial trisection task, individuals with a typical lateralization pattern ($median = -93.8, IQR = 142$) exhibited less spatial bias compared to both the mirrored ($median = 4.17, IQR = 135; T = -2.20, p = 0.025$) and the co-lateralization pattern groups ($median = 62.7, IQR = 164; T = -2.79, p = 0.012$). However, no significant differences in the number of words generation in verbal fluency task was observed among the groups ($ps > 0.05$). Further comparisons between the two lateralization patterns revealed that the co-lateralization pattern group ($median = -0.74, IQR = 1.20$) exhibited a lower overall dual-task performance compared to the complementary group ($median = 0.39, IQR = 2.01; W = 118, p = 0.056$; Suppl. Fig. 1C). In the CSTT, the co-lateralization group showed a significantly greater spatial bias ($median = 62.7, IQR = 164$) relative to the complementary group ($median = -6.71, IQR = 175, W = 243, p = 0.032$; Suppl. Fig. 1D) in the dual-task context, whereas no significant difference was observed in the verbal fluency task between the groups ($W = 158, p = 0.316$; Suppl. Fig. 1E).

3.3. The effect of lateralization pattern on behavioral interference

To assess behavioral interference, we measured the performance differences between dual-task and single-task conditions. Kruskal-Wallis tests were conducted after controlling for age, gender, and lateralization degree. These tests revealed significant effects of lateralization patterns on overall task interference ($\chi^2(2, N = 43) = 6.29, p = 0.043$, Fig. 4A) and on spatial interference ($\chi^2(2, N = 43) = 6.16, p = 0.046$, Fig. 4B). However, no significant effect was observed in the verbal fluency task ($\chi^2(2, N = 43) = 3.04, p = 0.219$, Fig. 4C). Post hoc comparisons showed that individuals with a typical lateralization pattern ($median = -0.41, IQR = 1.3$) exhibited less overall interference compared to those with a co-lateralization pattern ($median = 0.56, IQR = 1.11; T = -2.56,$

$p = 0.022$) and to those with a mirrored lateralization pattern ($median = 0.09, IQR = 1.80; T = -1.77, p = 0.063$). Specifically, for the CSTT in the dual-task context, individuals with a typical lateralization pattern ($median = -55.2, IQR = 67.9$) displayed significantly less spatial interference compared to those with a mirrored ($median = 19.5, IQR = 67; T = -2.57, p = 0.021$) and a co-lateralization pattern ($median = -5.06, IQR = 101; T = -1.61, p = 0.087$). However, in verbal fluency task, no significant differences in word generation interference were observed among the groups ($ps > 0.05$). Further comparison between two lateralization patterns revealed that greater overall dual-task interference in the co-lateralization pattern group ($median = 0.56, IQR = 1.11$) compared to the complementary pattern group ($median = -0.31, IQR = 2.01; W = 243, p = 0.032$; Suppl. Fig. 2A). In the verbal fluency task, the co-lateralization group ($median = 0.01, IQR = 0.88$) showed marginally greater word generation interference relative to the complementary group ($median = -0.09, IQR = 0.36; W = 225, p = 0.09$; Suppl. Fig. 2C). However, no significant differences were observed between these groups in the CSTT ($W = 193, p = 0.325$; Suppl. Fig. 2B).

To assess whether the lateralization degree influences on our main results, we conducted an additional analysis that did not control for this factor, while still controlling for age and gender (vs. the primary results, which also controlled for the degree). Suppl. Fig. 3 showed that the effects of lateralization patterns on behavioral performance in both dual-task and single verbal fluency task were mostly consistent with our main findings. In the single continuous spatial trisection task, the typical lateralization group exhibited significantly less spatial bias than the co-lateralization group and marginally less bias compared to the mirrored lateralization, aligning with the trends observed in the primary results. Furthermore, as depicted in Suppl. Fig. 4, the effect of lateralization patterns on overall performance interference in dual-task also aligned with the main analysis. Notably, while the above results showed the group effects were evident in CSTT but absent in verbal fluency task, the opposite was observed in the analysis without controlling for degree, where group effects were present in the verbal fluency but not in CSTT. Despite these, the patterns of group differences remained consistent across analyses. To control for the potential influence of executive

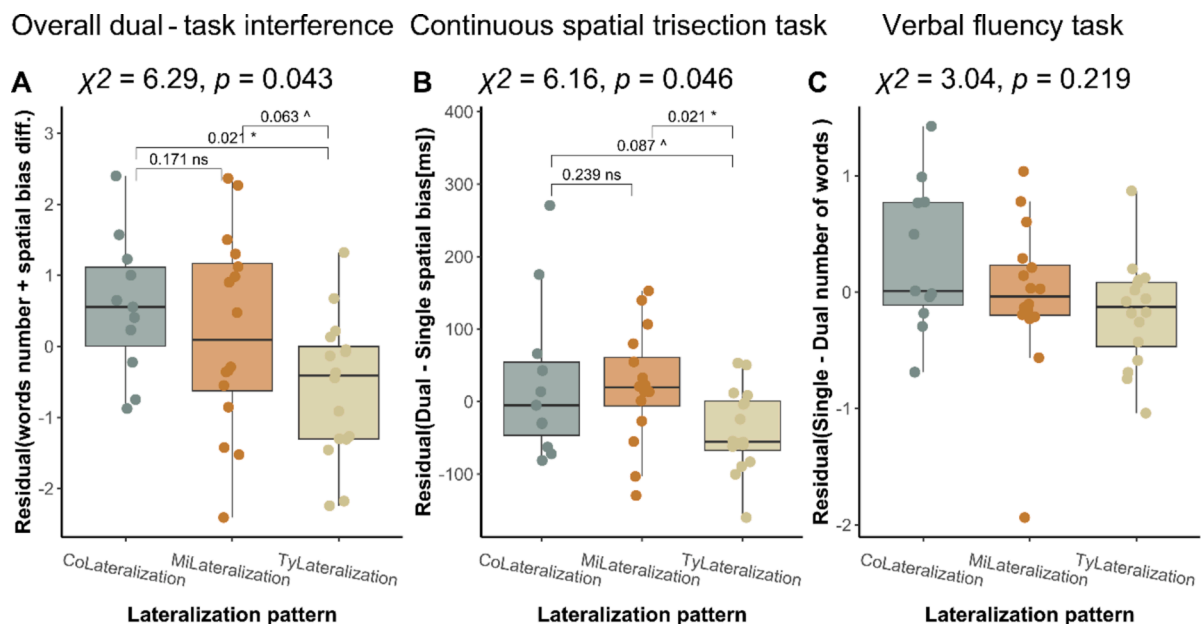


Fig. 4. Impact of lateralization patterns on dual-task interference. (A) The typical lateralization pattern group showed a significantly less overall interference compared to the co-lateralization pattern group, and a marginally less overall interference compared to the mirrored lateralization group. (B) In the continuous spatial trisection task, the typical lateralization pattern group showed a marginally less interference compared to the co-lateralization pattern group and a significantly less interference compared to the mirrored lateralization group. (C) In the verbal fluency task, there were no significant differences were observed among the groups in dual-task interference. Age, gender, and degree of lateralization were regressed out. Statistical significance is indicated by * for $p < 0.05$ and \wedge for marginally significant.

function on our results, the Kruskal-Wallis test was conducted to examine the effect of laterality pattern on stop-signal reaction time. No significant group differences were found.

3.4. The relationship between lateralization patterns and the FDC of the corpus callosum

To further investigate the role of the corpus callosum in influencing the lateralization patterns, two analyses were conducted. First, to examine the differences in combined fiber density and fiber-bundle cross-section of the corpus callosum across groups, Wilcoxon tests were performed, controlling for age and gender. Significant differences were observed in rostral body of the corpus callosum between individuals with a compensatory lateralization pattern and those with a co-lateralization pattern ($W = 813, p = 0.045$, Table 1). However, these differences were not statistically significant after further adjustment for the degree of lateralization ($W = 718, p = 0.243$, Table 1). Additional analyses controlling for non-interest variables across three groups also showed no significant differences (Suppl. Table 3).

Further investigations focused on the relationship between callosal connectivity and the degree of lateralization within different lateralization patterns. Spearman's rank correlation analyses indicated a negative correlation between the FDC of the Rostrum ($r = -0.333, p = 0.008$, Table 2) and the Rostral body ($r = -0.252, p = 0.048$, Table 2) of the corpus callosum in the complementary pattern group, after controlling for age and gender. Upon adjusting for the false discovery rate, the correlation in the rostrum subdivision was marginally significant ($p_{FDR} = 0.056$). Conversely, no significant correlations were observed for the co-lateralization pattern group.

Table 1
Comparison of complementary lateralization pattern and co-lateralization pattern on FDC in the subdivisions of the corpus callosum.

Subdivisions	Regress out age and gender		Regress out age, gender and LI	
	W	P	W	P
Rostrum	647	0.519	592	0.7334
Genu	707	0.281	645	0.5271
Rostral body	813	0.045	718	0.243
Anterior midbody	756	0.137	651	0.5021
Posterior midbody	694	0.328	613	0.6566
Isthmus	658	0.473	623	0.6174
Splenium	577	0.782	559	0.8337

Note. FDC: combined fiber density and fiber-bundle cross-section. Complementary lateralization pattern: included typical and mirrored lateralization pattern. W: W Mann-Whitney statistic, p: uncorrected p value. LI: lateralization indices.

Table 2
Spearman correlations between the FDC of the corpus callosum subdivisions and the combined lateralization degree across different lateralization patterns.

Subdivisions	Complementary Pattern			Co-lateralization pattern	
	r	P	P _{fdr}	r	P
Rostrum	-0.33	0.008	0.056	0.15	0.518
Genu	-0.19	0.136	0.271	-0.04	0.862
Rostral body	-0.25	0.048	0.168	-0.02	0.922
Anterior midbody	-0.15	0.232	0.271	-0.11	0.638
Posterior midbody	-0.10	0.456	0.456	-0.20	0.381
Isthmus	-0.18	0.171	0.271	0.03	0.907
Splenium	-0.16	0.224	0.271	0.03	0.889

Note. r: spearman's rank correlation coefficient, p: uncorrected p value, p_{FDR}: Adjusted P-value using Benjamini-Hochberg false discovery rate.

4. Discussion

This study aimed to investigate the association between lateralization patterns of two functions (language production and spatial attention) and behavioral performance as well as the relationship between these patterns and the corpus callosum. First, our results revealed that in the dual-task condition, individuals with a co-lateralization pattern exhibited marginally reduced overall performance compared to those with a typical lateralization pattern. Second, for cognitive interference, individuals with a co-lateralization pattern showed greater overall interference than those with a typical lateralization pattern. However, no such differences in interference effects were identified between individuals with a mirrored lateralization pattern and those with a co-lateralization pattern. Third, regarding the corpus callosum, no differences in the callosal connectivity were observed between the groups. However, a negative correlation was found between the degree of lateralization and the FDC of the corpus callosum's rostrum in the complementary pattern group.

The behavioral advantage of the typical lateralization pattern observed in the dual-task supports our hypothesis and aligns with findings from Rogers et al. (2004), who noted enhanced cognitive efficiency through hemispheric lateralization in a chick model. Our study extends these observations to humans, indicating that left language lateralization and right spatial attention facilitate parallel processing more effectively than when both functions are co-lateralized in the same hemisphere. This contrasts with a few previous dual-task studies on language and driving (Lust et al., 2011b) and language and mental rotation (Zickert et al., 2021), where no significant differences were reported between lateralization groups. These discrepancies may be attributed to reduced complexity, diminished simultaneity requirement, and the lack of continuity of the measurements. Furthermore, although the mirrored lateralization group also exhibited separate lateralization for language and spatial functions, their overall performance did not differ from those with a co-lateralization pattern, challenging the assumed benefits of functional segregation. This suggests that factors beyond parallel processing in atypical mirrored pattern may influence performance (see below). Additionally, no significant differences in single-task performance were observed across groups, consistent with previous findings from both animal and human studies (Cai et al., 2013; Häberling et al., 2011; Rogers et al., 2004; Villar-Rodríguez et al., 2024a). Collectively, these findings underscore that the impact of lateralization patterns on performance primarily emerges during simultaneous hemispheric engagement in different tasks.

Consistent with our hypothesis, the co-lateralization pattern group exhibited greater overall behavioral interference compared to the typical lateralization pattern group. This suggests that crowding two function networks within one hemisphere increases cognitive interference due to the competition of limited neutral resources. While Lust et al. (2011) initially reported similar findings, subsequent studies from their laboratory failed to replicate these results, likely due to limitations in their experimental paradigms. Notably, significant differences in performance interference was observed only in the continuous spatial trisection task, not in the verbal fluency task. This aligns with the findings from Strauss et al. (1990), which linked visuospatial attention deficit to the co-lateralization of language to the right hemisphere following brain lesions. To further explore the task-specific differences underpinning this interference effect, we calculated the percentage change between dual and single-task performance. An 8.78 % reduction in the number of words generated and a 63.1 % increase in spatial bias. This suggests that the CSTT is inherently more difficult and requires a higher allocation of cognitive resources, thereby magnifying the observed group differences in this task. Contrary to the parallel processing hypothesis, our results revealed a marginally significant difference in overall interference between the two complementary pattern groups. This suggests that functional segregation of different systems alone cannot fully account for the observed behavioral variations. The

dissociation between the function and structural asymmetry (Leroy et al., 2015; Zhu et al., 2024), along with potential genetic factors (Bishop, 2013), may jointly contribute to shaping the behavioral outcomes.

The language and spatial attention functions examined represent two distinct systems, each with separate control mechanisms for the left and right hemispheres. These mechanisms are critical for the synchronization and precise coordination of bilateral bodily activities (Kosslyn, 1987). Furthermore, these systems potentially seed the lateralization of related functions within the same hemisphere. For instance, studies have demonstrated that a right-lateralized language production is often accompanied by right-lateralized words recognition and tool use network (Cai & Van der Haegen, 2015; Vingerhoets et al., 2013), which are vital processes related to the language system. Functional segregation of different systems alone does not solely influence overall behavior. The consistency of lateralization among related sub-components within the same system may also be associated with the behavioral outcomes (Bradshaw et al., 2020; Parker et al., 2022). For instance, Bradshaw et al. (2020) examined the relationship between the lateralization pattern of three language subprocesses and language abilities, revealing a higher incidence of inconsistent patterns in individuals with developmental disorders. Incorporating the lateralization of different subprocesses within a system will provide insights into the absence of behavioral advantages in the mirrored lateralization pattern observed in this study.

Despite the behavioral disadvantages associated with atypical lateralization patterns, these patterns have been observed across a diverse range of animal species (see Güntürkün & Ocklenburg, 2017; Rogers, 2021 for reviews). For instance, in the context of motor control, Hopkins et al. (2003) found that while a majority of chimpanzees displayed a preference for using right hand in coordinated bimanual tasks, a subset showed a preference for the left. The distribution of these lateralization patterns within specific animal populations tends to stabilize at an equilibrium point (Vallortigara, 2006). The preservation of these traits through natural selection cannot be sufficiently explained by aforementioned mechanisms. At the population level, Vallortigara and Rogers (2005) posited that frequency-dependent fitness benefits might play a role, specifically the advantages conferred by being in the minority. For example, prey that move in atypical directions are more likely to evade predators more successfully, as predators anticipate the more common movement patterns of the majority (Vallortigara & Rogers, 2005). Moreover, it has been proposed that while atypical-lateralized individuals may gain significant advantages in social interactions at the population level, these do not outweigh the benefits of enhanced brain efficiency observed in typical-lateralized ones at the individual level (Ghirlanda et al., 2009; Ghirlanda & Vallortigara, 2004; Rogers, 2021).

Our study found no significant group differences in any subdivisions of the corpus callosum, contradicting the findings of Häberling et al. (2011). We observed only a subtle difference in the rostral body of the corpus callosum between individuals with a co-lateralization pattern and those with a complementary lateralization pattern. This suggests that crowding within the same hemisphere requires competition for neutral resources, potentially leading to enhanced interhemispheric connectivity as a compensation mechanism. This is supported by the increased callosal integrity observed in individuals with left hemisphere tumors (Tantillo et al., 2016). Moreover, our results revealed a negative correlation between callosal connectivity and the degree of functional lateralization, aligning with several previous studies (Bartha-Doering et al., 2021; Karolis et al., 2019; Labache et al., 2020; Villar-Rodríguez et al., 2024a). This finding provides additional evidence supporting the hypothesis that the corpus callosum plays an excitatory role in establishing functional lateralization by facilitating the information integration between the hemispheres. These results are consistent with the theory posited by Ringo et al. (1994), which claimed that the expansion of brain size during evolution resulted in delays in interhemispheric

conduction, thereby driving the hemispheric specialization for functions requiring high temporal resolution.

Furthermore, our results revealed that the mirrored lateralization group exhibited no significant difference in cognitive interference compared to the co-lateralization group. This suggests that the relationship between lateralization patterns and interference mechanism may be more complex than previously assumed. As discussed above, while the lateralization patterns within the language system may contribute to the behavioral outcomes observed in individuals with a mirrored pattern, further investigation into the structural basis underlying this pattern may offer additional insights. Previous research has demonstrated that atypical right lateralization of language does not necessarily correspond to mirrored asymmetries in gray matter or fiber pathways (Gerrits et al., 2022; Greve et al., 2013; Leroy et al., 2015; Vernooij et al., 2007; Zhu et al., 2024). Additionally, although callosal connections are closely associated with functional lateralization across multiple domains, the specific functions involved remain a subject of debate (Karolis et al., 2019; van der Knaap & van der Ham, 2011). In a prior study, Wang et al. (2020) investigated the functional lateralization of face processing at the structural connectome level. They found a correlation between the ratio of inter- and intra-hemispheric white matter connectivity and functional lateralization. Future research should further explore the function-structure relationship at a whole-brain connectivity level (Villar-Rodríguez et al., 2024b; Wang et al., 2019; Wu et al., 2022), which could provide deeper insights into the mechanisms underlying various lateralization patterns and their impacts on function-behavior relationships.

One limitation of the current study is the relatively small sample size. Despite the use of behavioral pre-screening to select participants with atypical lateralization, only a subset participated in the subsequent dual-tasks. Future research should aim to increase the sample size to enhance the robustness. Furthermore, due to time constraints during the fMRI sessions, we were unable to include dual-task assessments, limiting our ability to observe potential neutral crowding in co-lateralization patterns. Despite these limitations, our study introduces a dual-task paradigm of moderate difficulty, applicable not only to healthy adults but also potentially to clinical populations. This approach could contribute to assessing the extent of functional deficits due to lesion-induced neural plasticity and assessing cognitive efficiency in children during the development of functional lateralization. Language lateralization typically shifts from a bilateral to a left-lateralized pattern with age (Olulade et al., 2020). This shift is linked to changes in callosal connection integrating the bilateral language network (Bartha-Doering et al., 2021). Furthermore, lateralization patterns for different functions vary between children and adults, reflecting a developmental trajectory from an immature to a mature state (Liu et al., 2024). These findings suggest that examining lateralization patterns could provide valuable insights into brain maturation and development. Additionally, although our results revealed that the effect of lateralization pattern on task performance was not confounded by inhibitory control, further investigation into other components of executive function, such as working memory and cognitive flexibility, is necessary to confirm the findings. Furthermore, the absence of fMRI data for the dual-task condition limits our ability to fully elucidate the role of the domain-specific network and the multiple demand network in cognitive interference across different lateralization patterns. Further research is needed to fill this gap and to investigate more deeply the neural mechanisms underlying dual-task processing.

5. Conclusions

In examining language production and spatial attention, our findings indicate a reduced behavioral performance and increased interference in the co-lateralization pattern group compared to the typical lateralization pattern group under dual-task conditions. Notably, these group differences were primarily observed in the continuous spatial trisection task, which demanded greater cognitive effort than the verbal fluency

task. However, these differences were not apparent in the single-task conditions. Moreover, no significant effects on overall performance and interference were found between the co-lateralization and mirrored lateralization groups. Additionally, no significant group differences in callosal connectivity were detected among the three groups. Overall, our results only partially support the crowding and parallel processing hypotheses. A more comprehensive approach, such as examining the patterns of subprocesses within and across different systems, may yield further insights.

CRedit authorship contribution statement

Miaomiao Zhu: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Formal analysis, Data curation, Conceptualization. **Qing Cai:** Writing – review & editing, Validation, Supervision, Software, Resources, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.bandl.2025.105537>.

Data availability

Data will be made available on request.

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